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SEPTEMBER 30, 2004 ★ VOLUME 55 ★ NUMBERS 13-25

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# PROCEEDINGS

OF THE

## CALIFORNIA ACADEMY OF SCIENCES



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SAN FRANCISCO, CALIFORNIA

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On its return from the Galapagos expedition in November 1906, the Schooner *Academy* had in its hold an abundance of scientific specimens obtained by the scientists-crew during the 17-month long sojourn in the islands. Little did anyone realize that when the expedition departed San Francisco in June 1905 that the collections that the expedition would bring back to San Francisco would, in fact, form the nucleus of the Academy's new research collections. Nearly all that had been gathered previously, dating from the Academy's founding in 1853, was destroyed in the earthquake and fire that engulfed the city of San Francisco on 18 April 1906. When the expedition returned, Academy staff proceeded to wall off a part of the severely damaged old museum building to serve as a temporary warehouse for its precious collections. The photograph here shows the area in which the 258 tortoises brought back by the expedition were stored until the old museum building, which was slated for demolition a short time later, required that the specimens be moved to a new temporary site in a vacant downtown warehouse

ISSN 0068-547X

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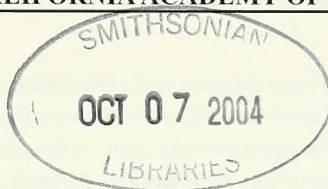
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Published by the California Academy of Sciences  
Golden Gate Park, San Francisco, California 94118 U.S.A.

Printed in the United States of America by  
Allen Press Inc., Lawrence, Kansas 66044





# **Annotated Listing of Diatom Types in Rabenhorst's *Die Algen Europa's* 1848–1882, and a Consideration of Their Nomenclatural Status**

**J.P. Kociolek**

*Diatom Collection, California Academy of Sciences, 875 Howard Street,  
San Francisco, CA 94103 USA; Email: pkociolek@calacademy.org*

Accumulation and dissemination of diatom collections during the 19<sup>th</sup> century were a significant means for diatomists to establish new taxa and communicate with the community of fellow researchers about the diversity of diatoms through space and time. The exsiccatae sets of Van Heurck (1882–1885), Cleve and Möller (1877–1882), Tempère and Peragallo (1889–1895; 1907–1915) and H.L. Smith (1876–1888) are relatively well known, but sets were also distributed by Wartmann and Schenk (1862–1882), M'Calla (1848) and Eulenstein (1867–1869). The materials distributed included at least some processed diatoms made into permanent slides or as raw material dried onto paper or mica.

Another relatively well-known exsiccatae set, that followed more in the tradition of phycology, bryology, mycology and lichenology was distributed not as processed slides, but as raw material. This set, which included more than 2500 numbers and is known as “*Die Algen Europas*,” was developed and distributed by Ludwig Rabenhorst (Fig. 1) between 1848 and 1882 (Rabenhorst 1848–1860, 1861–1882). Material included came from all over Europe as well as from far away places such as India, Burma, New Zealand and Honduras. The set formed the basis of numerous investigations by Rabenhorst and a wide range of collaborators, some immediately recognizable to diatomists (e.g., Grunow, Janisch, and Hilse) and others not so well known (Reinsch, Bleisch, Schwarz, and Hantzsch, after whom the genus *Hantzschia* was named). These sets were distributed widely, and may be found in herbaria across North America and the world.

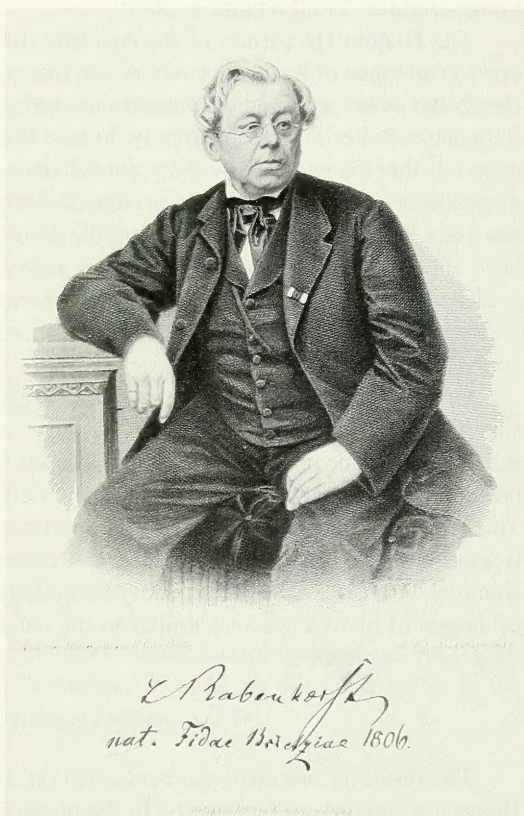


FIGURE 1. Ludwig Rabenhorst. From an engraving in *Flora Europaea Algarum* (1864). Courtesy Department of Botany, National Museum of Natural History, Washington, D.C.



From these samples, Rabenhorst and colleagues observed what they believed to be new taxa. In some cases, the taxa were identified as such on the labels of the exsiccatae; in other cases, the material was the basis for separate scientific publications. In some cases in both cases, the exsiccatae and separate publications, were notices for new taxa. According to the International Code of Botanical Nomenclature (Greuter et al. 2000, Articles 32 and 42.2), distribution of exsiccatae sets satisfies the requirement of effective publication, but the sole listing of names as new taxa without illustration or description does not satisfy the requirement of valid publication. The presentation of names in the exsiccatae set of Rabenhorst was not consistent. In some cases, descriptions accompanied the listing of the new taxon. In more rare situations, illustrations were included with the labels and descriptions. Frequently, the listing of names was without descriptions or illustrations. A similar situation to the listing of names only in exsiccatae was recently described for the exsiccatae slide set of Tempère and Peragallo (Servant-Vildary et al. 2001). Recent taxonomic workers have also accessed the exsiccatae and described new taxa from the material (e.g., Krammer and Lange-Bertalot 1988; Krammer 2000).

The Diatom Herbarium of the Academy of Natural Sciences of Philadelphia (ANSP) developed a catalogue of the types contained in that collection (Mahoney and Reimer 1987, 1997). They listed taxa described from the Rabenhorst exsiccatae as types in ANSP. The approach taken to the Rabenhorst material was, apparently, to take the exsiccatae labels at face value, without consideration whether the name was validly published or not. The treatment in Mahoney and Reimer (1997) of new taxa in the Rabenhorst exsiccatae is uneven, attributing species to Rabenhorst where others are listed as the author, not indicating the place of valid publication, listing of taxa that have not been validly published as well as missing many species either validly published in the exsiccatae or elsewhere. Recently, Robert Edgar of the Farlow Herbarium has developed a website where individual packets with printed material can be accessed (<http://www.huh.harvard.edu/diatom/pub-collfset.htm>).

Given the inconsistent way in which new taxa are treated in the Rabenhorst exsiccatae, and the superficial treatment in developing the type catalogue for ANSP, as well as the fact that the Rabenhorst exsiccatae contained type material for a wide range of diatom taxa, it was decided to present a detailed account of the types and new diatom names found in this interesting material. This work was also determined to be important, inasmuch as the number of catalogues of diatom types is relatively few (Mahoney and Reimer 1987, 1997; Williams 1988; Simonsen 1987; Kociolek et al. 1999; Servant-Vildary et al. 2001). This work should also facilitate a new planned catalogue of diatom species, similar to the catalogue of diatom genera published recently (Fourtanier and Kociolek 1999).

## METHODS AND APPROACH

The resulting research was conducted on the Rabenhorst exsiccatae contained in the Farlow Herbarium at Harvard University. In the present publication, a listing of samples that serve as the type material for new diatom taxa is detailed. We count four new genera and 233 new taxa at the level of species or lower. This contribution is presented in four parts, as follows: Part 1 includes those names that have been published in the exsiccatae; herein they are distinguished whether they are validly or invalidly published. This should help direct students and researchers to those taxa of interest that may be new and whose names require valid publication. For each sample, the following information is provided: exsiccatae serial number, the year of its distribution, locality data, taxon name with authority, date of publication and page number, and then any notes on the publication and taxonomic comments. Part 2 is an index of taxa and the exsiccatae number referenced



to the first part for both validly and invalidly published names. Part 3 summarizes the data for each name referenced in the first two parts; the names are presented alphabetically. Lastly, in Part 4, data are provided with respect to place of publication, date, pagination, and nomenclatural status of each name.

## PART 1. TYPE MATERIAL OF DIATOM NAMES IN THE RABENHORST EXSICCATAE.

### Validly Published Names

Exsiccatae Number: 383

Year Distributed: 1854

Locality Information: "Wasserfalles bei Schenpfenthal in Thüringen"

Taxon: *Melosira roeseana* Rabenhorst 1853, p. 13

Taxonomic Comments: Van Landingham (1971, p. 2241) indicates "Rabenhorst 1852, #382"

Exsiccatae Number: 403

Year Distributed: 1855

Locality Information: "Grosszschocker b. Leipzig in dem grossen Steinbruche, zwischen einem *Oedogonium*. 30. Aug. 1854"

Taxon: *Synedra interrupta* Auerswald in Rabenhorst 1855

Taxonomic Comments: A brief description accompanies the exsiccatae. This is the basionym of the name *Synedra splendens* var. *interrupta* (Auerswald) Rabenhorst 1864a, p. 134 and *S. ulna* var. *interrupta* (Auerswald) M. Peragallo 1903.

Exsiccatae Number: 505

Year distributed: 1856

Locality Information: "Wassermühlen bei Bergamo"

Publication Notes: A Latin description is included with the exsiccatae. See also Rabenhorst 1864a, p. 249, and Grunow 1860, p. 565.

Taxon: *Stauroneis rotaeana* Rabenhorst 1856, p. 103, pl. XIII, fig. 7 (without a description)

Exsiccatae Number: 561

Year Distributed: 1857

Locality Information: "Mineralwassern zu Canstatt, Temp. von 16–17° Reaum"

Taxon: *Falcatella zelleri* Rabenhorst 1857a

Taxonomic Comments: A brief description is included with the exsiccatae. Van Landingham (1969, p. 1646) indicates *F. zelleri* was described in Rabenhorst (1863a, p. 40). This taxon is the basionym for *Synedra zelleri* (Rabenhorst) Rabenhorst (1864a, p. 139).

Exsiccatae Number: 561

Year Distributed: 1857

Locality Information: "Mineralwassren zu Canstatt, Temp. von 16–17° Reaum"

Taxon: *Achnanthyidium thermale* Rabenhorst 1864a, p. 107

Exsiccatae Number: 604

Year Distributed: 1857

Locality Information: "In der Mergelgrube bei Peterwitz in der Nähe von Strehlen in Schlesien"

Taxon: *Cymbella helvetica* f. *silesiaca* Rabenhorst 1857a

Taxonomic Comments: A brief description is provided with the exsiccatae. Name not included in Van Landingham's *Catalogue*.



Exsiccatae Number: 611

Year Distributed: 1857

Locality Information: "Falaise"

Taxon: *Pinnularia falaiseana* Krammer 1992, p. 113

Publication Notes: Krammer (1992) indicates that H.L. Smith (1876–1888) slide 285 represents type material for this taxon.

Exsiccatae Number: 624

Year Distributed: 1857

Locality Information: "An feuchten Felsen beim Hirschensprung in Höllenthal (bei Freiburg im Br.)"

Taxon: *Gomphogramma rupestre* (Kützing) A. Braun ex Rabenhorst 1853, p. 33

Taxonomic Comments: This is a new combination of *Denticula thermale* Beta *rupestris* Kützing 1849. This does not appear to represent type material.

Exsiccatae Number: 625

Year Distributed: 1857

Locality Information: ". . . im Elbette . . ."

Taxon: *Nitzschia stagnorum* Rabenhorst 1857a

Taxonomic Comments: A Latin description is included with the exsiccatae. This name is the basionym of *Nitzschia thermalis* var. *stagnorum* (Rabenhorst) Rabenhorst 1864a.

Exsiccatae Number: 642

Year Distributed: 1857

Locality Information: "An *Leptomitus lacteus* bei Stuttgart . . ."

Taxon: *Surirella intermedia* Rabenhorst 1857b

Taxonomic Comments: A brief description accompanies the exsiccatae. *Surirella ovata* var. *intermedia* (Rabenh) Rabenhorst 1864a, p. 57, is based on this name.

Exsiccatae Number: 682b

Year Distributed: 1858

Locality Information: "Fossés pr. Falaise. De Brébisson"

Taxon: *Pinnularia viridula* (Kützing) Rabenhorst 1853, p. 43.

Taxonomic Comments: This is a new combination of *Frustulia viridula* Kützing 1833. This does not appear to represent type material.

Exsiccatae Number: 683

Year Distributed: 1858

Locality Information: "Marais de bois, Falaise"

Taxon: *Navicula major* var. *crassa* Brébisson ex Rabenhorst 1858a

Taxonomic Comments: Van Landingham's *Catalogue* (1975, p. 2658) lists the basionym of this taxon as "*Pinnularia major* var. *crassa* Rabenhorst 1848–1860; Rabenhorst 1864," with the combination in *Navicula* made by M. Peragallo (1903). This name appears in the exsiccatae in *Navicula*; transfer to *Pinnularia* was effected by Rabenhorst (1864a, p. 210).

Exsiccatae Number: 687

Year Distributed: 1858

Locality Information: ". . . se trouve en groupes assez épais sur les confervées. Falaise."

Taxon: *Synedra aggregata* Brébisson in Rabenhorst 1858a

Publication Notes: Exsiccatae provides a description in Latin of this taxon.



Exsiccatae Number: 688

Year Distributed: 1858

Locality Information: "Dresden"

Taxon: *Himantidium dilatatum* Wigand 1860, p. 43

Exsiccatae Number: 743

Year Distributed: 1858

Locality Information: "Auf *Vaucheria clavata* in der Ober-Lössnitz bei Dresden im sogen 'Walter's Grund'"

Taxon: *Gomphonema capitatum* var. *gracile* Rabenhorst 1858b

Taxonomic Comments: A very brief description in German is included with the exsiccatae. Name not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 761

Year Distributed: 1858

Locality Information: "Im Torfmoor am Titisee . . im badische Schwarzwalde"

Taxon: *Frustulia torfacea* A. Braun ex Rabenhorst 1853, p. 50

Taxonomic Comments: Specific epithet listed as "*torphacea*" in exsiccatae.

Exsiccatae Number: 765

Year Distributed: 1858

Locality Information: "Falaise"

Taxon: *Amphora ovalis* f. *nana* Rabenhorst 1864a, p. 92. The exsiccatae entry says "*Amphora ovalis* (Ehrbg.) Ktz."

Taxonomic Comments: The index to Rabenhorst (1864a, p. 327) indicates the name as "var. *nana*."

Exsiccatae Number: 781

Year Distributed: 1859

Locality Information: "Toofmoor bei Pohlenz, Oct. 1858"

Taxon: *Nitzschia arcus* Bulnheim 1859, p. 22

Exsiccatae Number: 801

Year Distributed: 1859

Locality Information: "Graben in Peissengrunde vor Neider-Hässlich bei Dresden"

Taxon: *Cylindrotheca* Rabenhorst 1859a

Publication Notes: This genus is described and figured in the exsiccatae.

Exsiccatae Number: 801

Year Distributed: 1859

Locality Information: "Graben in Peissengrunde vor Neider-Hässlich bei Dresden"

Taxon: *Cylindrotheca gerstenbergei* Rabenhorst 1859a.

Publication Notes: This species is described and figured in the exsiccatae.

Taxonomic Comments: This is the generitype for the new genus *Cylindrotheca*.

Exsiccatae Number: 802

Year Distributed: 1859

Locality Information: "auf Elbschlamm bei Dresden"

Taxon: *Navicula reinickeana* Rabenhorst 1859a

Publication Notes: A short description is provided with the exsiccatae. See also Rabenhorst 1863a, p. 35 for a description of this taxon.



Exsiccatae Number: 803

Year Distributed: 1859

Locality Information: "St. Gallen, in einem Brunnentrog im Klosterhof, den 15 January 1859"

Taxon: *Cymbella variabilis* Wartmann in Rabenhorst 1859a

Publication Notes: Description in German provided with the exsiccatae

Exsiccatae Number: 811

Year Distributed: 1859

Locality Information: "aus einem Feldbrunnen bei Peterwitz bei Strehlen in Schlesien"

Taxon: *Campylodiscus punctatus* Bleisch 1860, p. 29

Exsiccatae Number: 812

Year Distributed: 1859

Locality Information: "Strehlen in Schlesien, Ohlaufluss"

Taxon: *Stauroptera truncata* Rabenhorst 1853, pl. 9, fig. 12

Exsiccatae Number: 841

Year Distributed: 1859

Locality Information: "In einer Spalte des Chlorischieferfelsens am Franzensberge in Brünn"

Taxon: *Navicula nodosa* f. *curta* Rabenhorst 1864a, p. 207

Publication Notes: This name is listed as a "variety" in the index (p. 338). Rabenhorst lists *Navicula quinquerodes* Grunow 1860 as a synonym. It appears that Rabenhorst's is a new name for Grunow's taxon.

Exsiccatae Number: 842

Year Distributed: 1859

Locality Information: "mit *Sphagnum* umgürteten Tümpfel auf dem Eulengebirge bei Reichenbach in Schlesien"

Taxon: *Pinnularia rabenhorstii* Hilse 1860b, p. 82

Taxonomic Comments: Van Landingham (1978a, p. 3302) reports the specific epithet as "*rabenhorstiana* (Hilse in Rabenhorst 1859; Hilse 1960 [*sic*]) M. Peragallo 1903 p. 723."

Exsiccatae Number: 847

Year Distributed: 1859

Locality Information: "Petersdorf bei Gleiwitz in Schlesien . . ." [Poland]

Taxon: *Pleurostauron acutum* (W. Smith) Rabenhorst 1859c, Plate 1, fig. B, Plate 2, fig. F

Taxonomic Comments: Rabenhorst 1864a (p. 259) indicates this is a new combination for Smith's taxon. This does not appear to represent type material.

Exsiccatae Number: 848f

Year Distributed: 1859

Locality Information: "Um Gleiwitz in Schlesien . . ." [Poland (Katowice) Gliwice]

Taxon: *Stauroneis janischii* Rabenhorst 1859b

Publication Notes: A description in German and figure are provided with the exsiccatae.

Exsiccatae Number: 943

Year Distributed: 1860

Locality Information: "Dresden, in der Oberlössnitz in Mai 1859"

Taxon: *Nitzschia hantzschiana* Rabenhorst 1860a, p. 40

Publication Notes: The exsiccatae also includes a brief description. It is also described in Grunow (1862, p. 576)



Exsiccatae Number: 944

Year Distributed: 1860

Locality Information: "in einem Bache bei Tharandt (Sachsen)"

Taxon: *Nitzschia clausii* Hantzsch 1860b, p. 40

Publication Notes: The exsiccatae also includes a brief description. Descriptions of this taxon can also be found in Grunow (1862, p. 573, 559) and Rabenhorst (1863a, p. 48).

Exsiccatae Number: 945

Year Distributed: 1860

Locality Information: "Oberlössnitz bei Dresden, in einem Wasserbassin auf Steinem im September 1859"

Taxon: *Nitzschia media* Hantzsch 1860b, p. 40

Publication Notes: The exsiccatae also includes a brief description. Grunow (1862, p. 576) also provides a description for this taxon.

Exsiccatae Number: 946

Year Distributed: 1860

Locality Information: "in einem Tümpel bei Mortizburg bei Dresden im September 1859"

Taxon: *Nitzschia gracilis* Hantzsch 1860b, p. 40

Publication Notes: The exsiccatae also includes a brief description. See Grunow (1862, p. 560, 575) for a description of this taxon.

Exsiccatae Number: 947

Year Distributed: 1860

Locality Information: "Oberlössnitz bei Dresden auf Wurzeln und Steinem in einem Wasserbassin"

Taxon: *Navicula macrogongyla* Rabenhorst 1860a, p. 40

Taxonomic Comments: The exsiccatae does not indicate the specific epithet of the new *Navicula*, but it is given in the publication.

Exsiccatae Number: 949

Year Distributed: 1860

Locality Information: "In Gräben um Dresden häufig von Gerstenberger"

Taxon: *Nitzschia communis* Rabenhorst 1860b

Publication Notes: See Grunow (1862, p. 561, 578) and Rabenhorst (1864a, p. 159) for descriptions of this taxon.

Taxonomic Comments: There is reference to an effectively published illustration, (*Hedwigia* 1860, pl. 6, fig. 3). It appears from the text of the exsiccatae that this is to be a new name for a diatom identified by Gerstenberger (in *Hedwigia*) as *Synedra frustulium* Kützinger.

Exsiccatae Number: 950

Year Distributed: 1860

Locality Information: "Am Galgenberge bei Strehlen in Schlesien"

Taxon: *Nitzschia minuta* Bleisch in Rabenhorst 1860b

Taxonomic Comments: A description accompanies the exsiccatae. See also Bleisch 1863, p. 78 and Grunow 1862, p. 578.

Exsiccatae Number: 951

Year Distributed: 1860

Locality Information: "in einem einzigen Brunnen bei Strehlen an der Strasse nach Striege"

Taxon: *Pinnularia gibba* f. *curta* Bleisch in Rabenhorst 1860b

Taxonomic Comments: A brief description is provided with the exsiccatae. The exsiccatae packet lists this taxon as "*Pinnularia gibba* forma *curta*, varietas nova". This name is not listed in Van Landingham's *Catalogue* as either a variety or a form of *P. gibba*.

Exsiccatae Number: 952

Year Distributed: 1860

Locality Information: "in einem Brunnen an der Strasse von Riegersdorf nach Strehlen"

Taxon: *Pinnularia medioconstricta* Bleisch in Rabenhorst 1860b

Publication Notes: A description is provided with the exsiccatae. See also Bleisch 1863, p. 81.

Exsiccatae Number: 953

Year Distributed: 1860

Locality Information: "in einem Graben auf dem Rücken der Eule . . . October 1859"

Taxon: *Pinnularia hilseana* Janisch in Rabenhorst 1860b

Publication Notes: A description is provided with the exsiccatae. See also Hilse 1860b, p. 82.

Exsiccatae Number: 954

Year Distributed: 1860

Locality Information: "Ohlauffluss bei Strehlen in Schlesien unter Oscillarien; im Juli 1859"

Taxon: *Pinnularia silesiaca* Bleisch in Fresenius 1862

Publication Notes: See also Bleisch 1863, p. 81 and Bleisch in Rabenhorst 1863a, p. 38.

Taxonomic Comments: A description is lacking in the exsiccatae.

Exsiccatae Number: 958

Year Distributed: 1860

Locality Information: "im Züricher See bei der Badeanstalt"

Taxon: *Encyonema prostratum* f. *helvetica-robustior* Rabenhorst 1860b

Taxonomic Comments: The name is listed as "*Encynonema prostratum* forma *helvetica robustior*."

A short description is provided, and reference to a previous description and figures qualifies as a valid publication for this name. Name not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 962

Year Distributed: 1860

Locality Information: "Steinbrüchen am Galgenberge bei Strehlen"

Taxon: *Stauroneis cohnii* Hilse in Rabenhorst 1860b

Taxonomic Comments: A brief description is included with the exsiccatae. See also Hilse 1860b, p. 83.

Exsiccatae Number: 963

Year Distributed: 1860

Locality Information: "in altern Steinbrüchen am Galgenberge bei Strehlen"

Taxon: *Stauroneis undulata* Hilse 1860, p. 83

Taxonomic Comments: A brief description is included with the exsiccatae.

Exsiccatae Number: 984

Year Distributed: 1860

Locality Information: "In einem Sumpfe in Kaitzer Grunde bei Dresden"

Taxon: *Nitzschia tryblionella* Hantzsch in Rabenhorst 1860c

Publication Notes: A description is included with the exsiccatae.



Exsiccatae Number: 1003

Year Distributed: 1861

Locality Information: "in einem Quellwasser bei Salem"

Taxon: *Achnantheidium jackii* Rabenhorst 1861a

Publication Notes: Latin description provided with the exsiccatae. This name is also proposed in Rabenhorst 1864a, p. 106, but the description differs significantly enough from the exsiccatae that two separate species might be described under the same name from the same material.

Exsiccatae Number: 1021b

Year Distributed: 1861

Locality Information: "[in den Mergelgruben von] Peterwitz bei Strehlen in Schlesien"

Taxon: *Epithemia goeppertiana* Hilse 1860, p. 79

Publication Notes: This diatom is described in the exsiccatae under the number 1021 and listed under 1021b.

Exsiccatae Number: 1022

Year Distributed: 1861

Locality Information: "von Holmachern zur Erlangung von Trinkwasser angelegten Rinne auf dem Rücken der Eule (bei Reichenbach in Schlesien)"

Taxon: *Cyclotella hilseana* Rabenhorst 1864a, p. 33

Taxonomic Comments: This was originally listed with the exsiccatae as *Cyclotella dubia* Hilse in Rabenhorst, a name also published in Hilse 1860, p. 79. A note with the exsiccatae indicates "Ob die Pflanze gar ein neues Genus bildet, wie ich sast vermuthet, dürfte wohl die Zukunft Ichren."

Exsiccatae Number: 1023

Year Distributed: 1861

Locality Information: "Pfungsten 1860 auf dem Rücken der Eule in einer höhe von 3000 F"

Taxon: *Pinnularia sudetica* Hilse 1860, p. 82

Taxonomic Comments: This diatom is described in the exsiccatae. Van Landingham (1978a, p. 3324) lists this taxon as "*Navicula sudetica* Hilse 1861 p. 82; Hilse in Rabenhorst 1861–1879 No. 1023" and "*Pinnularia sudetica* (Hilse) M. Peragallo 1903, p. 725". Krammer (2000) designated this material as the lectotype of Hilse's taxon.

Exsiccatae Number: 1024

Year Distributed: 1861

Locality Information: "Brunnenabfluss von Katschwitz bei Strehlen"

Taxon: *Synedra campyla* Hilse 1860, p. 84

Publication Notes: A brief description is also provided with the exsiccatae.

Exsiccatae Number: 1025

Year Distributed: 1861

Locality Information: "im Ziegengrunde bei Strehlen"

Taxon: *Pinnularia ovalis* Hilse 1860, p. 82

Publication Notes: A description is also provided with the exsiccatae.

Exsiccatae Number: 1026

Year Distributed: 1861

Locality Information: "in den Mergelgruben von Gross-Lauden bei Strehlen"

Taxon: *Epithemia intermedia* Hilse 1860, p. 76

Publication Notes: A description is also provided with the exsiccatae.

Taxonomic Comments: This name is an earlier homonym of *Epithemia intermedia* Fricke 1904

Exsiccatae Number: 1041

Year Distributed: 1861

Locality Information: "Dresden, im artefischen Brunnen"

Taxon *Fragilaria mesolepta* Rabenhorst 1861b

Publication Notes: Exsiccatae provides Latin description.

Exsiccatae Number: 1045

Year Distributed: 1861

Locality Information: "in Gräben bei Canstatt"

Taxon: *Surirella suevica* Zeller in Rabenhorst 1861b

Publication Notes: Exsiccatae provides Latin and German descriptions. See Krammer & Lange-Bertalot 1987, p. 89.

Exsiccatae Number: 1046

Year Distributed: 1861

Locality Information: "Gegend von Marburg"

Taxon: *Himantidium striatum* Wigand 1860, p. 43

Exsiccatae Number: 1046

Year Distributed: 1861

Locality Information: "Gegend von Marburg"

Taxon: *Synedra arcuatum* Wigand 1860, p. 43

Taxonomic Comments: This name is an earlier homonym for *Synedra arcuatum* Cleve-Euler 1953, p. 68.

Exsiccatae Number: 1065

Year Distributed: 1861

Locality Information: "Bochla pr. Grossenhain (Saxoniae) in fossis pratorum"

Taxon: *Cymbella naviculiformis* Auerswald ex Heiberg 1863

Publication Notes: No description provided in exsiccatae.

Taxonomic Comments: See the interpretation of the nomenclature of this taxon by Reimer (pp. 31–32 in Patrick & Reimer 1975).

Exsiccatae Number: 1066

Year Distributed: 1861

Locality Information: "Um Leipzig, in der Elster und im Teiche bei Barneck"

Taxon: *Pleurosigma gracilentum* Rabenhorst 1861b

Publication Notes: A short description is provided with the exsiccatae. See also Rabenhorst 1863a, p. 617 and Rabenhorst 1864a, p. 240.

Taxonomic Comments: Van Landingham (1978a, p. 3375) lists this as "Rabenhorst 1861–1879, No. 166".

Exsiccatae Number: 1084

Year Distributed: 1861

Locality Information: "St. Gallen, in einem Brunnentrog des Zweibrücher Tobels"

Taxon: *Odontidium hiemale* f. *rotundata* Rabenhorst 1864a, p. 116

Taxonomic Comments: This taxon was listed with the exsiccatae as "*Odontidium mesodon* Kütz.



form!" Van Landingham (1978a, p. 3154) indicates the basionym of this taxon is *O. rotundatum* Rabenhorst 1853 (p. 34, plate 2, fig. 4c), although this name is used in the figure legends for plate 2, fig. 4c, the listing of this taxon name on page 34 is under *O. hyemale*. The name *O. rotundatum* Rabenhorst is a later homonym of *O. rotundatum* (Ehrenb.) Kütz. 1849.

Exsiccatae Number: 1088

Year Distributed: 1861

Locality Information: "in einem kleinen Teiche bei St. Gallen (Schweiz)"

Taxon: *Epithemia rabenhorstii* Wartmann in Rabenhorst 1861c

Publication Notes: A brief description is provided with the exsiccatae.

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 1089

Year Distributed: 1861

Locality Information: "bei St. Gallen in einem kleinen Teiche auf Mühlegg"

Taxon: *Epithemia zebra* var. *intermedia* Wartmann in Rabenhorst 1861c

Publication Notes: A brief description is provided with the exsiccatae.

Taxonomic Comments: This name is also presented in Rabenhorst 1864a, p. 65. This name is not included in Van Landingham's *Catalogue*. It is an earlier homonym for the combination made by Hustedt (1934).

Exsiccatae Number: 1101

Year Distributed: 1861

Locality Information: "Am Elbufer im Gehege bei Dresden"

Taxon: *Pleurosigma scalproides* Rabenhorst 1861d

Publication Notes: Description and illustration provided in exsiccatae.

Exsiccatae Number: 1104

Year Distributed: 1861

Locality Information: "Elbufer im grossen Gehege bei Dresden"

Taxon: *Diatoma gracillimum* Hantzsch in Rabenhorst 1861d

Publication Notes: Description and illustration are provided in the exsiccatae.

Taxonomic Comments: The specific epithet was originally listed as "*gracillimum*", but this should probably be considered a typographical error. Van Landingham's *Catalogue* (1969, p. 1295) lists the specific epithet as "*gracillimum*".

Exsiccatae Number: 1106

Year Distributed: 1861

Locality Information: "Walther's Grund in der Oberlössnitz"

Taxon: *Pinnularia peracuminata* Krammer 2000

Exsiccatae Number: 1107

Year Distributed: 1861

Locality Information: "Dresden, im artefischen Brunnen"

Taxon: *Cocconema pachycephalum* Rabenhorst 1861d

Publication Notes: Description and illustrations provided in exsiccatae. Rabenhorst (1863a, p. 616) had created the superfluous name *Cocconema robustum* for this taxon. Krammer (2002) has recently renamed this taxon *Cymbella hantzschiana* Krammer.

Exsiccatae Number: 1114

Year Distributed: 1861

Locality Information: "Oberlössnitz bei Dresden"

Taxon: *Nitzschia tumida* Hantzsch in Rabenhorst 1861e

Publication Notes: A specimen is figured with the exsiccatae. Mahoney & Reimer (1997) indicate this species is described in Rabenhorst 1864a (p. 153).

Exsiccatae Number: 1161

Year Distributed: 1861

Locality Information: "Strehlen in Schlesien . . . Jordansmühle"

Taxon: *Pleurostaurum lineare* Hilse 1860b, p. 83

Publication Notes: A description is provided with the exsiccatae.

Exsiccatae Number: 1164

Year Distributed: 1861

Locality Information: "Im Marmorbruch zu Prieborn bei Strehlen in Schlesien"

Taxon: *Nitzschia perpusilla* Rabenhorst 1861f

Publication Notes: See also Rabenhorst 1864a, 159.

Taxonomic Comments: A brief Latin description is included with the exsiccatae. Van Landingham (1978a, p. 3096) lists this taxon occurring in exsiccatae number 1163.

Exsiccatae Number: 1166

Year Distributed: 1861

Locality Information: "in einem Graben bei Teppendorf in Schlesien"

Taxon: *Cymbella maculata* var. *major* Rabenhorst 1864a, p. 80

Taxonomic Comments: According to Rabenhorst in comments accompanying the exsiccatae, this diatom was initially identified as *Cymbella lunula* (Ehrenb.) Rabenhorst 1853, p. 23. Van Landingham (1969, p. 1210) suggests the name *Cymbella lunula* Hilse in Rabenhorst was created in this exsiccatae number, but there is no indication from the exsiccatae that this combination was made.

Exsiccatae Number: 1167

Year Distributed: 1861

Locality Information: "Aus der Eule in einer Höhe von gegen 3000 Fuss, im October 1860"

Taxon: *Eunotia minuta* Hilse 1860, p. 79

Publication Notes: A description is also provided with the exsiccatae.

Exsiccatae Number: 1183

Year Distributed: 1861

Locality Information: "im städtischen granitnen Röhrtröge zu Strehlen in Schlesien"

Taxon: *Stauroneis goeppertiana* Bleisch ex Rabenhorst 1861g

Publication Notes: A description is provided with the exsiccatae. See also Bleisch 1863, p. 81.

Exsiccatae Number: 1201

Year Distributed: 1861

Locality Information: "Dresden, Prinz Georg's Garten 1861"

Taxon: *Cymatopleura nobilis* Hantzsch 1860a, p. 36

Publication Notes: Illustrations provided with exsiccatae.

Exsiccatae Number: 1203

Year Distributed: 1861

Locality Information: "Krippengrund i.d. sächs. Schweiz"



Taxon: *Pinnularia rupestris* Hantzsch ex Rabenhorst 1861h

Publication Notes: A description is provided with the exsiccatae.

Exsiccatae Number: 1208

Year Distributed: 1861

Locality Information: "in einem Quelle beim Göthe-Häuschen auf dem Gückelhahn in Thüringer Walde"

Taxon: *Surirella thuringiacea* Hantzsch in Rabenhorst 1861h

Publication Notes: A description is provided with the exsiccatae.

Exsiccatae Number: 1246

Year Distributed: 1862

Locality Information: "in einem Bach in Höskler bei Zürich"

Taxon: *Cocconema variabile* Cramer ex Rabenhorst 1862a

Publication Notes: A description is provided with the exsiccatae.

Exsiccatae Number: 1246

Year Distributed: 1862

Locality Information: "in einem Bach in Höskler bei Zürich"

Taxon: *Cymbella vulgata* Krammer 2002, p. 55

Exsiccatae Number: 1248

Year Distributed: 1862

Locality Information: "Mühlegg bei St. Gallen (Schweiz)"

Taxon: *Encyonema maximum* Wartmann ex Rabenhorst 1862a

Publication Notes: A description is provided with the exsiccatae.

Exsiccatae Number: 1261

Year Distributed: 1862

Locality Information: "bei Gerbersdorf in Schlesien"

Taxon: *Cymbella minuta* Hilse in Rabenhorst 1862b

Publication Notes: See also Hilse 1863, p. 66.

Taxonomic Comments: Krammer (1997, p. 54) points out the error made by Reimer (in Patrick & Reimer 1975, p. 42) about the exsiccatae number where this taxon was published.

Exsiccatae Number: 1263

Year Distributed: 1862

Locality Information: "in einem Graben bei Hussinetz bei Strehlen"

Taxon: *Pinnularia viridis* var. *coerulescens* Hilse in Rabenhorst 1862b

Publication Notes: See also Hilse 1863, p. 68.

Taxonomic Comments: A brief description is included in the exsiccatae. This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 1266

Year Distributed: 1862

Locality Information: "in einem Graben im Dorfe Hussinetz bei Strehlen"

Taxon: *Nitzschia thermalis* var. *minor* Hilse in Rabenhorst 1862b

Publication Notes: See also Hilse 1860, p. 67.

Taxonomic Comments: Van Landingham (1978a, p. 3128) indicates this taxon was published by Hilse in 1860.

Exsiccatae Number: 1267

Year Distributed: 1862

Locality Information: "in einem Graben hinter dem Walde von Dobergast bei Strehlen in Schlesien"

Taxon: *Nitzschia kuetzingiana* Hilse in Rabenhorst 1862b

Taxonomic Comments: *Nitzschia kuetzingii* Rabenhorst 1864 is the valid name for this taxon.

Exsiccatae Number: 1268

Year Distributed: 1862

Locality Information: "in einem Graben am Teiche von Hussinetz bei Strehlen"

Taxon: *Stauroneis anceps* f. *gracilis* Rabenhorst 1864a, p. 247

Exsiccatae Number: 1283

Year Distributed: 1862

Locality Information: "Dresden, in Prinz Georgs Garten"

Taxon: *Nitzschia recta* Hantzsch in Rabenhorst 1862c

Publication Notes: A brief diagnosis is provided in the exsiccatae.

Taxonomic Comments: Van Landingham gives year of publication as "1861–1879".

Exsiccatae Number: 1283

Year Distributed: 1862

Locality Information: "Dresden, in Prinz Georgs Garten"

Taxon: *Navicula rotundata* Hantzsch in Rabenhorst 1862c

Publication Notes: A brief description is provided in the exsiccatae.

Exsiccatae Number: 1301

Year Distributed: 1862

Locality Information: "am obersten Gräberhause Sulza"

Taxon: *Homoeocladia bulbosissima* Rabenhorst 1862d

Publication Notes: A description of this taxon is provided with the exsiccatae. The species is also described in Rabenhorst 1863a, p. 617 and Rabenhorst 1864a, p. 167.

Exsiccatae Number: 1321

Year Distributed: 1862

Locality Information: "Dresden, im artefischen Brunnen"

Taxon: *Cocconeis nanum* Hantzsch in Rabenhorst 1862e

Publication Notes: A description is provided with the exsiccatae.

Exsiccatae Number: 1322

Year Distributed: 1862

Locality Information: "Strehlen bei Dresden, in einem Graben"

Taxon: *Sphenella naviculoides* Hantzsch in Rabenhorst 1862e

Publication Notes: A description is provided with the exsiccatae.

Exsiccatae Number: 1323

Year Distributed: 1862

Locality Information: "Dresden, im Abflüsse des artefischen Brunnens"

Taxon: *Synedra amphirhynchus* var. *undulata* Rabenhorst 1862e

Publication Notes: See also Rabenhorst 1864a, p. 134.



Exsiccatae Number: 1381

Year Distributed: 1862

Locality Information: "Ruisseaux et fossés. Falaise"

Taxon: *Surirella crumena* Brébisson ex Kützing 1849

Taxonomic Comments: Rabenhorst 1864a, p. 57 says No. 1381 is "specimen authen." Krammer in Krammer & Lange-Bertalot (1987, p. 96) designates this material as the lectotype for the name of the species.

Exsiccatae Number: 1385

Year Distributed: 1862

Locality Information: "Bei Leipzig"

Taxon: *Encyonema auerswaldii* Rabenhorst 1853a, p. 24

Exsiccatae Number: 1386

Year Distributed: 1862

Locality Information: "San Giuliano prope Genuam, ad sax leg. Dufour"

Taxon: *Homoeocladia dufourii* DeNotaris in DeNotaris & Baglietto 1871

Exsiccatae Number: 1403

Year Distributed: 1862

Locality Information: "Ostindische Diatomeen. Von Algen und Meeresschlamm aus dem ostindischen Archipel"

Taxon: *Climacosphenia indica* Hantzsch 1863, p. 18

Exsiccatae Number: 1403

Year Distributed: 1862

Locality Information: "Ostindische Diatomeen. Von Algen und Meeresschlamm aus dem ostindischen Archipel"

Taxon: *Synedra pulcherrima* Hantzsch 1863, p. 19

Exsiccatae Number: 1403

Year Distributed: 1862

Locality Information: "Ostindische Diatomeen. Von Algen und Meeresschlamm aus dem ostindischen Archipel"

Taxon: *Synedra formosa* Hantzsch 1863, p. 19

Exsiccatae Number: 1403

Year Distributed: 1862

Locality Information: "Ostindische Diatomeen. Von Algen und Meeresschlamm aus dem ostindischen Archipel"

Taxon: *Toxarium rostratum* Hantzsch 1863, p. 19

Exsiccatae Number: 1403

Year Distributed: 1862

Locality Information: "Ostindische Diatomeen. Von Algen und Meeresschlamm aus dem ostindischen Archipel"

Taxon: *Mastogloia interrupta* Hantzsch 1863, p. 20

Exsiccatae Number: 1403

Year Distributed: 1862

Locality Information: "Ostindische Diatomeen. Von Algen und Meeresschlamm aus dem ostindischen Archipel"

Taxon: *Nitzschia formica* Hantzsch 1863, p. 20

Taxonomic Comments: Figure legend on p. 22 says "*Tryblionella formica*", and Hantzsch indicates this species is identical with *Nitzschia tryblionella* in Rabenhorst exsiccatae 984.

Exsiccatae Number: 1403

Year Distributed: 1862

Locality Information: "Ostindische Diatomeen. Von Algen und Meeresschlamm aus dem ostindischen Archipel"

Taxon: *Eupodiscus minutus* Hantzsch 1863, p. 20

Exsiccatae Number: 1403

Year Distributed: 1862

Locality Information: "Ostindische Diatomeen. Von Algen und Meeresschlamm aus dem ostindischen Archipel"

Taxon: *Cocconeis heteroidea* Hantzsch 1863, p. 20

Exsiccatae Number: 1405

Year Distributed: 1862

Locality Information: "im Polenzthale (sächs. Schweiz)"

Taxon: *Synedra bicurvata* Biene ex Rabenhorst 1863b

Publication Notes: There is a reference to an illustration (*Nitzschia arcus* Bulnheim in *Hedwigia* II, Tafel II, fig. 1) to validate the name. This taxon was described in Rabenhorst 1864a, p. 129.

Exsiccatae Number: 1421

Year Distributed: 1863

Locality Information: "Kraussnitz bei Grossenhain in Sachsen, in einem moorigen Wiesengraben"

Taxon: *Surirella saxonica* Auerswald in Rabenhorst 1863b

Publication Notes: A Latin description is provided with the exsiccatae. See also Rabenhorst 1864a, p. 53.

Exsiccatae Number: 1441

Year Distributed: 1863

Locality Information: "aus eine Bache unweit Sennerei unterhalb Casaccio auf dem Kukmanier"

Taxon: *Cymbella elegans* Cramer 1863, p. 65

Exsiccatae Number: 1441

Year Distributed: 1863

Locality Information: "aus eine Bache unweit Sennerei unterhalb Casaccio auf dem Kukmanier"

Taxon: *Fragilaria* [*Fragillaria* in exsiccatae] *undulata* Cramer 1863, p. 65

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "Meeralgen von Honduras"

Taxon: *Amphitetras cruciata* Janisch & Rabenhorst 1863, p. 4

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "[Meeralgen] an den Küste von Honduras"



Taxon: *Campylodiscus rabenhorstianus* Janisch in Janisch & Rabenhorst 1863, p. 6

Publication Notes: This name was published earlier by Grunow (1862).

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "[Meeralgen] an den Küste von Honduras"

Taxon: *Amphitetras parvula* Janisch & Rabenhorst 1863, p. 4

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "[Meeralgen] an den Küste von Honduras"

Taxon: *Climacosphenia linearis* Janisch & Rabenhorst 1863, p. 6

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "[Meeralgen] an den Küste von Honduras"

Taxon: *Cocconeis kirchenpaueriana* Janisch & Rabenhorst 1863, p. 7

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "[Meeralgen] an den Küste von Honduras"

Taxon: *Cocconeis flexella* Janisch & Rabenhorst 1863, p. 7

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "[Meeralgen] an den Küste von Honduras"

Taxon: *Denticella ventricosa* Janisch & Rabenhorst 1863, p. 8

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "[Meeralgen] an den Küste von Honduras"

Taxon: *Navicula bleischiana* Janisch & Rabenhorst 1863, p. 9

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "[Meeralgen] an den Küste von Honduras"

Taxon: *Navicula janischiana* Rabenhorst in Janisch & Rabenhorst 1863, p. 10

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "[Meeralgen] an den Küste von Honduras"

Taxon: *Navicula marina* Janisch & Rabenhorst 1863, p. 10

Taxonomic Comments: *Non Navicula marina* Ralfs in Pritchard 1861

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: "[Meeralgen] an den Küste von Honduras"

Taxon: *Synedra gomphonema* Janisch & Rabenhorst 1863, p. 13

Exsiccatae Number: 1481

Year Distributed: 1863

Locality Information: “[Meeralgen] an den Küste von Honduras”

Taxon: *Tessella hyalina* Janisch & Rabenhorst 1863, p. 13

Exsiccatae Number: 1489

Year Distributed: 1863

Locality Information: “Brunnen bei Weiselwitz bei Strehlen”

Taxon: *Surirella diaphana* Bleisch ex Rabenhorst 1863c

Publication Notes: Short description provided with exsiccatae. See also Bleisch 1863, p. 78 and Rabenhorst 1864a, p. 55.

Exsiccatae Number: 1492

Year Distributed: 1863

Locality Information: “Brunnen an der Mühle zu Toeppendorf bei Strehlen in Schlesien”

Taxon: *Diatoma elongatum* var. *abbreviatum* Rabenhorst 1864a, p. 122

Exsiccatae Number: 1501

Year Distributed: 1863

Locality Information: “Am einem Blumentopfe, melcher in einem Warnhause längere Zeit in einem Napfe mit Wasser gestanden”

Taxon: *Epithemia minuta* Hantzsch in Rabenhorst 1863d

Publication Notes: A description is provided with the exsiccatae.

Exsiccatae Number: 1503a

Year Distributed: 1863

Locality Information: “In einer Cisterne, . . . in dem Chloritschieferfelsen des Franzensberges in Brunn”

Taxon: *Nitzschia dubia* var. *minor* Grunow 1862, p. 568

Exsiccatae Number: 1503a

Year Distributed: 1863

Locality Information: “In einer Cisterne, . . . in dem Chloritschieferfelsen des Franzensberges in Brunn”

Taxon: *Nitzschia constricta* f. *minor* Rabenhorst 1864a, p. 153

Exsiccatae Number: 1561

Year Distributed: 1863

Locality Information: “In dem kalten reissenden Wasser der Aare bei Interlaken”

Taxon: *Synedra frigida* Zeller in Rabenhorst 1863e

Publication Notes: A description is provided with the exsiccatae.

Taxonomic Comments: This name is not included in Van Landingham’s *Catalogue*.

Exsiccatae Number: 1651

Year Distributed: 1864

Locality Information: “Am Ziegenberg bei Husiant [*sic* ? = Hussinetz] in Schlesien”

Taxon: *Nitzschia bleischi* Janisch in Bleisch 1863, p. 78

Publication Notes: This taxon is illustrated in the exsiccatae.

Taxonomic Comments: Van Landingham (1978a, p. 3019) gives the publication as Rabenhorst “1848–1860”.

Exsiccatae Number: 1700

Year Distributed: 1864



Locality Information: "Dresden"

Taxon: *Pinnularia parvillissima* Krammer 2000

Exsiccatae Number: 1701

Year Distributed: 1864

Locality Information: "In stagnis turfosis prope Neukirch Lusatae superioris legit M. Rostock"

Taxon: *Cymbella cuspidata* f. *maxima* Rabenhorst 1864d

Publication Notes: A brief description is provided in Latin. The name was presented originally as *Cymbella cuspidata* var. *naviculiformis* f. *maxima*.

Exsiccatae Numbers: 1711 and 1712

Year Distributed: 1864

Locality Information: "An Pfählen des Hafendammes von Ostende, grüne incrustirende Ueberzüge. Juli 1861. Grunow coll."

Taxon: *Nitzschia incrustans* Grunow 1862, p. 566

Publication Notes: Krammer & Lange-Bertalot (1988, p. 246) discuss the lectotype of this taxon.

Exsiccatae Number: 1716

Year Distributed: 1864

Locality Information: "Incrustirend auf Pflanzenstengeln in Nildelta"

Taxon: *Amphora tumidula* Grunow in Rabenhorst 1864a, p. 175

Publication Notes: A Latin description accompanies the exsiccatae.

Exsiccatae Number: 1718

Year Distributed: 1864

Locality Information: "Timsah See (bittersalzhaltig) bei Ismailia, Nildelta"

Taxon: *Nitzschia schweinfurthii* Grunow in Rabenhorst 1864a, p. 175

Publication Notes: A Latin description and "nov. spec." accompany this name. This is the basionym of *Nitzschia obtusa* var. *schweinfurthii* (Grunow) Grunow in Cleve & Grunow 1880.

Exsiccatae Number: 1725

Year Distributed: 1864

Locality: Austria, "In einem kleinen See am Ufer der Donau im Prater bei Wien"

Taxon: *Surirella gracilis* (W. Smith) Grunow 1862

Publication Notes: See Krammer & Lange-Bertalot (1988, p. 189, plates 136, figures 1–4).

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia formica* var. *elongata* Grunow 1865, p. 3

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia formica* var. *genuina* Grunow 1865, p. 3

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia formica* var. *intermedia* Grunow 1865, p. 3

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia formica* var. *bigibba* Grunow 1865, p. 3

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia ventricosa* var. *elongata* Grunow 1865, p. 4

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia camelus* var. *genuina* Grunow 1865, p. 4

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia camelus* var. *didymodon* Grunow 1865, p. 4

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia camelus* var. *denticulata* Grunow 1865, p. 4

Exsiccatae Number: 1727 Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia indica* Grunow 1865, p. 5

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia indica* var. *ventralis* Grunow 1865, p. 5

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia major* var. *sexundulata* Grunow 1865, p. 5

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia major* var. *undulata* Grunow 1865, p. 16, pl. 1, fig. 8

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia major* var. *octoundulata* Grunow 1865, p. 5, pl. 1, fig. 8

Exsiccatae Number: 1727

Year Distributed: 1864



Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia pectinalis* var. *undulata* f. *biundulata* Grunow 1865, p. 4, pl. 1, fig. 5a

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia pectinalis* var. *undulata* f. *quadriundulata* Grunow 1865, p. 4, pl. 1, fig. 5b [PK confirmed]

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia pectinalis* var. *undulata* f. *octoundulata* Grunow 1865, p. 4, pl. 1, fig. 5c

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Desmogonium rabenhorstianum* Grunow 1865, p. 6

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Encyonema gerstenbergeri* Grunow 1865, p. 9

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Gomphonema turris* var. *apiculatum* Grunow 1865, p. 10

Exsiccatae Number: 1765

Year Distributed: 1865

Locality Information: "In aquis frigidis prope Insbruck"

Taxon: *Odontidium alpigenum* A.J. Kerner ex Rabenhorst 1865b

Publication Notes: A Latin description is provided with the exsiccatae.

Exsiccatae Number: 1802

Year Distributed: 1865

Locality Information: "im Brunnentroge des Gehöftes in Sedlitz bei Strehlen"

Taxon: *Cymbella silesiaca* Bleisch in Rabenhorst 1865c.

Publication Notes: A description is provided with the exsiccatae.

Exsiccatae Number: 1804

Year Distributed: 1865

Locality Information: "Westgalizien, Jeziorki bei Chrzanów"

Taxon: *Nitzschia schliephackeana* Grunow ex Rabenhorst 1864a, p. 324

Publication Notes: See also Rabenhorst 1866c, p. 56.

Exsiccatae Number: 1806

Year Distributed: 1865

Locality Information: "Diatomaceen-Erde, Nottingham Maryland, U.S. (Bermuda Tripel aut.)"

Taxon: *Heliopelta ehrenbergii* Eulenstein ex Rabenhorst 1865c

Publication Notes: Though no formal description is offered, reference to previous descriptions, here in the form of three previous descriptions of Ehrenberg, suffice to validate this name. The name is, however, illegitimate inasmuch as Eulenstein should have used one of Ehrenberg's epithets.

Exsiccatae Number: 1891

Year Distributed: 1866

Locality Information: "In fossis humidis sylvae Sebaldianae (Reichsforst) prope Neuhoof (Norimbergae) in Franconia"

Taxon: *Nitzschia* [*Nitzschia* on exsiccatae label] *franconica* Reinsch in Rabenhorst 1866a

Taxonomic Comments: A Latin description is part of the exsiccatae.

Exsiccatae Number: 1891

Year Distributed: 1866

Locality Information: "In fossis humidis sylvae Sebaldianae (Reichsforst) prope Neuhoof (Norimbergae) in Franconia"

Taxon: *Nitzschia* [*Nitzschia* on exsiccatae label] *franconica* var. *serpentina* Reinsch in Rabenhorst 1866a

Taxonomic Comments: A Latin description is part of the exsiccatae.

Exsiccatae Number: 1895

Year Distributed: 1866

Locality Information: "in Tuberi fluminis locis leniter fluentibus infra Rubromontum in Franc"

Taxon: *Cocconeis striolata* f. *substriolata* Reinsch in Rabenhorst 1866a

Publication Notes: A description and illustrations accompany the exsiccatae.

Exsiccatae Number: 1912

Year Distributed: 1866

Locality Information: "In per sylvis ductis fossis sempiterne humidis sylvae Sebaldianae (Reichsforst) infra 'Kalkreuth' in Franconia"

Taxon: *Melosira paffiana* Reinsch in Rabenhorst 1866b

Publication Notes: A Latin description and illustrations accompany the exsiccatae. See also Reinsch 1866, p. 11.

Exsiccatae Number: 1933

Year Distributed: 1866

Locality Information: "Weisengräben unter Eis bei Eibenstock"

Taxon: *Denticula quadrata* Kuntze in Rabenhorst 1866c

Publication Notes: A description is provided with the exsiccatae.

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 1934

Year Distributed: 1866

Locality Information: "einer Bucht des salzigen See's bei Halle"

Taxon: *Amphora bulnheimii* Rabenhorst 1866c

Publication Notes: A brief diagnosis is provided with the exsiccatae.

Exsiccatae Number: 1998

Year Distributed: 1867

Locality Information: "Molér, . . . aus der Insel Mors in nördlichen Jütland"

Taxon: *Triceratium heibergianum* Grunow 1866, p. 145



Taxonomic Comments: Van Landingham (1978b, p. 4047) considers this diatom conspecific with *T. heibergii* Grunow in Van Heurck 1883.

Exsiccatae Number: 1998

Year Distributed: 1867

Locality Information: "Molér, . . . aus der Insel Mors in nördlichen Jütland"

Taxon: *Triceratium jensenianum* Grunow 1866, p. 145

Exsiccatae Number: 1998

Year Distributed: 1867

Locality Information: "Molér, . . . aus der Insel Mors in nördlichen Jütland"

Taxon: *Stephanogonia danica* Grunow 1866, p. 146

Exsiccatae Number: 1998

Year Distributed: 1867

Locality Information: "Molér, . . . aus der Insel Mors in nördlichen Jütland"

Taxon: *Sceptroneis gemmata* Grunow 1866, p. 146

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Podosphenia remulus* Grunow 1867, p. 2

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Asterionella bleakeleyi* var. *notata* Grunow 1867, p. 2

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Synedra undosa* Grunow 1867, p. 4

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Synedra cuneata* Grunow 1867, p. 5

Taxonomic Comment: *Non Synedra cuneata* Ehrenberg 1834

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Striatella intermedia* Grunow 1867, p. 6

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Striatella lindigiana* Grunow 1867, p. 6

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Plagiodiscus* Grunow & Eulenstein in Grunow 1867, p. 8

Publication Notes: This is the original publication of the genus name *Plagiodiscus*.

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Plagiodiscus nervatus* Grunow 1867, p. 8

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Berkeleya fusidium* Grunow 1867, p. 17

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Nitzschia affinis* f. *major* Grunow 1867, p.18

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Nitzschia kolaczekii* Grunow 1867, p.18.

Publication Notes: See also Grunow 1877, p. 173.

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Bacillaria tropica* Grunow 1867, p.19

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Rhoicosigma* Grunow 1867, p. 19

Publication Notes: This is the original publication of the genus name *Rhoicosigma*.

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Rhoicosigma reichardtianum* Grunow 1867, p.19

Taxonomic Comment: This is equivalent to *Rhoicosigma reichardtii* Grunow 1877, p. 181.

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Rhoicosigma reichardtianum* var. *constrictum* Grunow 1877, p. 181.

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Amphora decussata* Grunow 1867, p. 23



Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Amphora hemisphaerica* Grunow 1867, p. 24

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Amphora cymbelloides* Grunow 1867, p. 24

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Navicula reticulata* Grunow 1867, p. 26

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Navicula triundulata* Grunow 1867, p. 27

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Schizostauron* Grunow 1867, p. 28

Publication Notes: This is the original publication of the genus name *Schizostauron*.

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Schizostauron lindigianum* Grunow 1867, p. 28

Publication Notes: See also Grunow 1877.

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Licmophora gracilis* var. *borealis* Grunow 1867, p. 34

Taxonomic Comments: This name is actually a new combination for *Rhipidophora borealis* Kützing 1844 and should be presented as *Licmophora gracilis* var. *borealis* (Kützing) Grunow 1867; the Rabenhorst exsiccatae does not appear to be original Kützing material.

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Isthmia lindigiana* Grunow & Eulenstein in Grunow 1867, p. 29

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: The name was originally offered as "*Triceratium (orbiculatum* Shadbolt?) *elongata*" Grunow 1867, p. 31. Validly published names from this are *Triceratium elongatum* Grunow 1867 or *Triceratium orbiculatum* var. *elongatum* (Grunow) Grunow 1877

Exsiccatae Number: 2000

Year Distributed: 1867

Locality Information: "von *Sargassum* aus der Rückreife von Neu-Granada"

Taxon: *Licmophora gracilis* var. *constricta* Grunow 1867, p. 34

Exsiccatae Number: 2005

Year Distributed: 1867

Locality Information: "Dives" [= Dives-sur-Mer, in Calvados]

Taxon: *Eupodiscus roperii* Brébisson in Rabenhorst 1867

Publication Notes: A description is provided in the exsiccatae. See also Brébisson 1870, p. 41.

Taxonomic Comments: The name is proposed as "*roperii*" though the correct spelling is "*roperi*." This a *nomen novum* for *Coscinodiscus ovalis* Roper 1858, required for its transfer to *Eupodiscus* since priority exists for *Eupodiscus ovalis* Norman 1861. The Rabenhorst material does not appear to be original material for any of these names.

Exsiccatae Number: 2012

Year Distributed: 1867

Locality Information: "Sallenelles (Calvados)"

Taxon: *Surirella ovata* var. *marina* Brébisson in Rabenhorst 1867

Publication Notes: A description is provided with the exsiccatae.

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 2061

Year Distributed: 1868

Locality Information: "Wiesengraben bei Quartschen"

Taxon: *Cymatopleura marchica* Hermann in Rabenhorst 1868

Publication Notes: A brief description is provided with the exsiccatae.

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 2150

Year Distributed: 1870

Locality Information: "de la baie du M. St. Michel, près d'Avranches"

Taxon: *Amphiprora arenaria* Brébisson in Rabenhorst 1870

Publication Notes: A description is provided with the exsiccatae. Van Landingham (1967, p. 160) gives question marks next to this name. He attributes it to Rabenhorst, but then indicates "Dec 217 according to Chase in Habirshaw (1885)" and "No. 2150 according to Mills (1934, p. 904)"; the entry actually occurs in Mills 1933, p. 129.

Exsiccatae Number: 2171

Year Distributed: 1870

Locality Information: "Hab. ad plantas submersas Galliae, prope Falaise, imprimis ad folia Sphagnum [sic]"

Taxon: *Peronia erinacea* Brébisson & Arnott in Kitton 1868, p. 16

Taxonomic Comments: This is a *nomen novum* for *Gomphonema fibula* Brébisson ex Kützing 1849, p. 65 (= *Peronia fibula* (Brébisson ex Kützing) Ross). *Peronia erinacea* is an illegitimate name.

Exsiccatae Number: 2172

Year Distributed: 1870

Locality Information: "Hab. in aquis submarinis Galliae: Dives, Trouville"

Taxon: *Navicula humerosa* Brébisson ex Wm. Smith 1856, p. 93



Exsiccatae Number: 2222

Year Distributed: 1870

Locality Information: "Ad thermas insulae Inarimes (Ischia)"

Taxon: *Denticula elegans* f. [*gamma*] *valida* Pedicino 1867, p. 7

Publication Notes: No description accompanies the exsiccatae.

Exsiccatae Number: 2261

Year Distributed: 1872

Locality Information: "Meeresgrundprobe, Carral bei Valdivia"

Taxon: *Navicula seminulum* var. *fragilarioides* Grunow in Van Heurck 1880, plate 14, fig. 10

Exsiccatae Number: 2264

Year Distributed: 1872

Locality Information: "Auf Algen beim Leuchthturme von Livorno"

Taxon: *Cocconeis pseudomarginata* var. *intermedia* Grunow 1868, p. 13

Exsiccatae Number: 2264

Year Distributed: 1872

Locality Information: "Auf Algen beim Leuchthturme von Livorno"

Taxon: *Cocconeis pellucida* var. *minor* Grunow 1868, p. 13

Exsiccatae Number: 2312

Year Distributed: 1873

Locality Information: "Calcutta"

Taxon: *Nitzschia kurzeana* Rabenhorst 1873

Publication Notes: A Latin description is provided with the exsiccatae.

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*. Reference is given to *N. kurzii* Rabenhorst ex Cleve & Möller #78.

Exsiccatae Number: 2331

Year Distributed: 1873

Locality Information: "Im Felsen am Meeresufer bei Akyab (Hauptstadt der Provinz Arracan)"

Taxon: *Podosira kurzii* Zeller 1873, p. 175.

Exsiccatae Number: 2357

Year Distributed: 1873

Locality Information: "Rangoon"

Taxon: *Eunotia kurzeana* Grunow in Möller 1881

Taxonomic Comments: The entry in Rabenhorst (1873) as *Eunotia kurziana* is an invalid name because it was published without a description. Possible orthographic variant of *E. kurzeana* Grunow in Möller 1881.

Exsiccatae Number: 2380

Year Distributed: 1874

Locality Information: "Küste von Japan"

Taxon: *Licmophora divisa* f. *japanica* Rabenhorst 1874

Publication Notes: A brief description accompanies the exsiccatae.

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 2382

Year Distributed: 1874

Locality Information: "Salzwasser Gräben bei Kaschan (Pers. med.)"

Taxon: *Nitzschia* [*Nitzschia* on label] *parvula* f. *elongata-gracilis* Hausknecht in Rabenhorst 1874

Publication Notes: A short description is provided with the exsiccatae.

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 2391

Year Distributed: 1874

Locality Information: "Grundprobe von Whampoa"

Taxon: *Triceratium sinense* Schwarz 1874, p. 163

Exsiccatae Number: 2391

Year Distributed: 1874

Locality Information: "Grundprobe von Whampoa"

Taxon: *Triceratium whampoense* Schwarz 1874, p. 163

Exsiccatae Number: 2481

Year Distributed: 1877

Locality Information: "Vera Cruz (zwischen Sertularien)"

Taxon: *Navicula lobata* Schwarz in Rabenhorst 1877

Publication Notes: A Latin description and illustration are provided with the exsiccatae.

Exsiccatae Number: 2483

Year Distributed: 1877

Locality Information: "Vera Cruz"

Taxon: *Navicula splendens* Schwarz in Rabenhorst 1877

Publication Notes: A description is provided with the exsiccatae. This taxon is illustrated in the materials accompanying No. 2481.

Taxonomic Comments: This name is not listed in Van Landingham's *Catalogue*

Exsiccatae Number: 2560

Year Distributed: 1878

Locality Information: "vom Mathuri-Pass auf Neu-Zeeland, c. 3000; hoch . . ."

Taxon: *Amphora berggrenii* Cleve 1881, p. 4

### Invalidly Published Names

Exsiccatae Number: 1041

Year Distributed: 1861

Locality Information: "Dresden, im artefischen Brunnen"

Taxon *Fragilaria hantzschiana* Gerstenberger in Rabenhorst 1861b

Publication Notes: Exsiccatae lacks a description.

Exsiccatae Number: 1249

Year Distributed: 1862

Locality Information: "Mitteloppaquelle auf dem Leiterberg im Gesenke (Mähren)"

Taxon: *Melosira distans* f. *articulis longioribus* Rabenhorst 1862a

Taxonomic Comments: Name not in Van Landingham's *Catalogue*. No description or illustration associated with the exsiccatae. It is not clear whether Rabenhorst intended this to be a new taxon.

Exsiccatae Number: 1489

Year Distributed: 1863

Locality Information: "Brunnen bei Weisselwitz bei Strehlen"

Taxon: *Amphora abbreviata* Bleisch in Rabenhorst 1864a, p. 55

Publication Notes: No description provided or reference to previous descriptions with exsiccatae.

Van Landingham's *Catalogue* (1967, p. 187) considers this name validly published in the exsiccatae, but no description and/or illustration is provided.

Exsiccatae Number: 1700

Year Distributed: 1864

Locality Information: "Dresden"

Taxon: *Pinnularia gibba* f. *minor* Rabenhorst 1864b

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia pectinalis* var. *undulata* f. *triundulata* Grunow 1865, p. 4

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia pectinalis* var. *undulata* f. *quinqueundulata* Grunow 1865, p. 4

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia pectinalis* var. *undulata* f. *septemundulata* Grunow 1865, p. 4

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia pectinalis* var. *undulata* f. *novemundulata* Grunow 1865, p. 4

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Eunotia pectinalis* var. *undulata* f. *sexundulata* Grunow 1865, p. 4

Exsiccatae Number: 1727

Year Distributed: 1864

Locality Information: "Insel Banka (Ostindien)"

Taxon: *Gomphonema dichotomum* var. *affine* f. *minor* Grunow 1865, p. 10

Exsiccatae Number: 1954

Year Distributed: 1867

Locality Information: "In den Torfgruben von Jentendorf und Quitzdorf, Kr. Rothenburg"

Taxon: *Frustulia saxonica* f. *turfacea* Hilse

Publication Notes: No description, illustrations or reference to other descriptions are provided with the exsiccatae.

Taxonomic Comments: Van Landingham (1971, p. 1848) equates this taxon with *Frustulia turfacea* A. Braun in Rabenhorst 1853, p. 50, yet no such relationship is indicated on the label exsiccatae number 1954.



Exsiccatae Number: 2025

Year Distributed: 1867

Locality Information: "Falaise"

Taxon: *Synedra lunaris* var. *elongata* Brébisson in Rabenhorst

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Publication Notes: No description is provided in the exsiccatae.

Exsiccatae Number: 2213

Year Distributed: 1870

Locality Information: "Eisenbahn-Ausstich bei Breslau"

Taxon: *Achnanthidium lanceolatum* var. *major* Rabenhorst 1870

Publication Notes: No description accompanies the exsiccatae.

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 2223

Year Distributed: 1870

Locality Information: "Ad algas majores maris Neapolitani circa insulan Caprearum"

Taxon: *Cocconeis parthenopaea* N.A. Pedicino in Rabenhorst 1870.

Publication Notes: No description accompanying the exsiccatae.

Exsiccatae Number: 2234

Year Distributed: 1870

Locality Information: "An der Ems unweit Emden"

Taxon: *Berkeleya dillwynii* var. *sericeum* Eiben in Rabenhorst 1870

Publication Notes: No description accompanies the exsiccatae.

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 2263

Year Distributed: 1872

Locality Information: "An der Küste der Insel S. Paul in der Südsee, Expedition Novara"

Taxon: *Cocconeis grevillei* var. *minor* Grunow in Rabenhorst 1872

Publication Notes: No description accompanies the exsiccatae.

Exsiccatae Number: 2353

Year Distributed: 1873

Locality Information: "Calcutta, Balliaghata Canal und saltlakes"

Taxon: *Nitzschia obtusa* var. *kurziana* Rabenhorst 1873

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 2353

Year Distributed: 1873

Locality Information: "Calcutta, Balliaghata Canal und saltlakes"

Taxon: *Navicula calcuttensis* Grunow in Rabenhorst 1873

Exsiccatae Number: 2353

Year Distributed: 1873

Locality Information: "Calcutta, Balliaghata Canal und saltlakes"

Taxon: *Pleurosigma kurzianum* Grunow in Rabenhorst 1873

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 2358

Year Distributed: 1873

Locality Information: "Rangoon-lake"

Taxon: *Nitzschia rangoonensis* Grunow

Publication Notes: No description accompanies the exsiccatae. Label is printed as 2558.

Taxonomic Comments: This name is not included in Van Landingham's *Catalogue*.

Exsiccatae Number: 2551

Year Distributed: 1878

Locality Information: "Quilly-Le-Vicomte (France) Dr. Ch. Manoury"

Taxon. *Nitzschia palea* f. *curta* Grunow

Publication Notes: Van Landingham (1978, p. 3089) indicates this name is published in Cleve & Möller 1878, No. 124, but this name is invalidly published in that exsiccatae set because it lacks a description.

## PART 2. TAXONOMIC NAME REGISTER

## (A) VALIDLY PUBLISHED NAMES

Taxon Name	Exsiccatae	Taxon Name	Exsiccatae
<i>Achnanthyidium jackii</i> Rabenhorst	1003	<i>Epithemia minuta</i> Hantzsch	1501
<i>Achnanthyidium lanceolatum</i> var. <i>major</i> Rabenhorst	2213	<i>Epithemia rabenhorstii</i> Wartmann	1088
<i>Achnanthyidium thermale</i> Rabenhorst	561	<i>Epithemia zebra</i> var. <i>intermedia</i> Wartmann	1089
<i>Amphiprora arenaria</i> Brébisson	2150	<i>Eunotia camelus</i> var. <i>denticulata</i> Grunow	1727
<i>Amphitetras cruciata</i> Janisch & Rabenhorst	1481	<i>Eunotia camelus</i> var. <i>didymodon</i> Grunow	1727
<i>Amphitetras parvula</i> Janisch & Rabenhorst	1481	<i>Eunotia camelus</i> var. <i>genuina</i> Grunow	1727
<i>Amphora berggrenii</i> Cleve	560	<i>Eunotia formica</i> var. <i>bigibba</i> Grunow	1727
<i>Amphora bulnheimii</i> Rabenhorst	1934	<i>Eunotia formica</i> var. <i>elongata</i> Grunow	1727
<i>Amphora cymbelloides</i> Grunow	2000	<i>Eunotia formica</i> var. <i>genuina</i> Grunow	1727
<i>Amphora decussata</i> Grunow	2000	<i>Eunotia formica</i> var. <i>intermedia</i> Grunow	1727
<i>Amphora hemisphaerica</i> Grunow	2000	<i>Eunotia indica</i> Grunow	1727
<i>Amphora ovalis</i> f. <i>nana</i> Rabenhorst	765	<i>Eunotia indica</i> var. <i>ventralis</i> Grunow	1727
<i>Amphora tumidula</i> Grunow	1716	<i>Eunotia kurzeana</i> Grunow in Möller	2357
<i>Asterionella bleakeyi</i> var. <i>notata</i> Grunow	2000	<i>Eunotia major</i> var. <i>undulata</i> Grunow	1727
<i>Bacillaria tropica</i> Grunow	2000	<i>Eunotia major</i> var. <i>sexundulata</i> Grunow	1727
<i>Berkeleya fusidium</i> Grunow	2000	<i>Eunotia major</i> var. <i>octoundulata</i> Grunow	1727
<i>Campylodiscus punctatus</i> Bleisch	811	<i>Eunotia minuta</i> Hilse	1167
<i>Campylodiscus rabenhorstianus</i> Janisch in Janisch & Rabenhorst	1481	<i>Eunotia pectinalis</i> var. <i>biundulata</i> Grunow	1727
<i>Climacosphenia indica</i> Hantzsch	1403	<i>Eunotia pectinalis</i> var. <i>undulata</i> f. <i>triundulata</i> Grunow	1727
<i>Climacosphenia linearis</i> Janisch & Rabenhorst	1481	<i>Eunotia pectinalis</i> var. <i>undulata</i> f. <i>octoundulata</i> Grunow	1727
<i>Cocconeis flexella</i> Janisch & Rabenhorst	1481	<i>Eunotia ventricosa</i> var. <i>elongata</i> Grunow	1727
<i>Cocconeis heteroidea</i> Hantzsch	1403	<i>Eupodiscus minutus</i> Hantzsch	1403
<i>Cocconeis kirchenpaueriana</i> Janisch & Rabenhorst	1481	<i>Eupodiscus roperi</i> Brébisson	2005
<i>Cocconeis pellucida</i> var. <i>minor</i> Grunow	2264	<i>Falcatella zelleri</i> Rabenhorst	561
<i>Cocconeis pseudomarginata</i> var. <i>intermedia</i> Grunow	2264	<i>Fragilaria mesolepta</i> Rabenhorst	1041
<i>Cocconeis striolata</i> f. <i>substriolata</i> Reinsch	1895	<i>Fragilaria undulata</i> Cramer	1441
<i>Cocconema nanum</i> Hantzsch	1321	<i>Frustulia torfacea</i> A. Braun ex Rabenhorst	761
<i>Cocconema pachycephalum</i> Rabenhorst	1107	<i>Gomphogramma rupestre</i> (Kützing) A. Braun ex Rabenhorst	624
<i>Cocconema variabile</i> Cramer	1246	<i>Gomphonema capitatum</i> var. <i>gracile</i> Rabenhorst	743
<i>Cyclotella dubia</i> Hilse	1022	<i>Gomphonema turris</i> var. <i>apiculatum</i> Grunow	1727
<i>Cyclotella hilseana</i> Rabenhorst	1022	<i>Heliopecta ehrenbergii</i> Eulenstein	1806
<i>Cylindrotheca Rabenhorst</i>	801	<i>Himantidium dilatatum</i> Wigand	688
<i>Cylindrotheca gerstenbergeri</i> Rabenhorst	801	<i>Himantidium striatum</i> Wigand	1046
<i>Cymatopleura marchica</i> Herrmann	2061	<i>Homeocladia bulnheimiana</i> Rabenhorst	1301
<i>Cymatopleura nobilis</i> Hantzsch	1201	<i>Homeocladia dufowii</i> DeNotaris in DeNotaris & Baglietto	1386
<i>Cymbella cuspidata</i> f. <i>maxima</i> Rabenhorst	1701	<i>Isthmia lindigiana</i> Grunow & Eulenstein	2000
<i>Cymbella elegans</i> Cramer	1441	<i>Licmophora divisa</i> f. <i>japonica</i> Rabenhorst	2380
<i>Cymbella hantzschiana</i> Krammer	1107	<i>Licmophora gracilis</i> f. <i>constricta</i> Grunow	2000
<i>Cymbella helvetica</i> f. <i>silesiaca</i> Rabenhorst	604	<i>Licmophora gracilis</i> f. <i>borealis</i> Grunow	2000
<i>Cymbella lunula</i> (Ehrenberg) Rabenhorst	1166	<i>Mastogloia interrupta</i> Hantzsch	1403
<i>Cymbella maculata</i> var. <i>major</i> Rabenhorst	1166	<i>Melosira pfaffiana</i> Reinsch	1912
<i>Cymbella minuta</i> Hilse	1261	<i>Melosira roeseana</i> Rabenhorst	383
<i>Cymbella naviculiformis</i> Auerswald ex Heiberg	1065	<i>Navicula bleischiana</i> Janisch & Rabenhorst	1481
<i>Cymbella silesiaca</i> Bleisch	1802	<i>Navicula humerosa</i> Brébisson in Wm. Smith	2172
<i>Cymbella variabilis</i> Wartmann	803	<i>Navicula janischiana</i> Rabenhorst	1481
<i>Cymbella vulgata</i> Krammer	1246	<i>Navicula lobata</i> Schwarz	2481
<i>Denticella ventricosa</i> Janisch & Rabenhorst	1481	<i>Navicula macrogongyla</i> Rabenhorst	947
<i>Denticula elegans</i> var. <i>valida</i> Pedicino	2222	<i>Navicula major</i> var. <i>crassa</i> Brébisson	683
<i>Denticula quadrata</i> Kuntze	1933	<i>Navicula marina</i> Janisch & Rabenhorst	1481
<i>Desmogonium rabenhorstianum</i> Grunow in Rabenhorst	1727	<i>Navicula nodosa</i> f. <i>curta</i> Rabenhorst	841
<i>Diatoma elongatum</i> var. <i>abbreviatum</i> Rabenhorst	1492	<i>Navicula reinickeana</i> Rabenhorst	802
<i>Diatoma gracillimum</i> Hantzsch	1104	<i>Navicula reticulata</i> Grunow	2000
<i>Encyonema auerswaldii</i> Rabenhorst	1385	<i>Navicula rotundata</i> Hantzsch	1283
<i>Encyonema gerstenbergeri</i> Grunow	1727	<i>Navicula seminulum</i> var. <i>fragilarioides</i> Grunow	2261
<i>Encyonema maximum</i> Wartmann	1248	<i>Navicula splendens</i> Schwarz	2483
<i>Encyonema prostratum</i> f. <i>helvetica-robustior</i> Rabenhorst	958	<i>Navicula triundulata</i> Grunow	2000
<i>Epithemia goeppertiana</i> Hilse	1021	<i>Nitzschia affinis</i> f. <i>major</i> Grunow	2000
<i>Epithemia intermedia</i> Hilse	1026	<i>Nitzschia arcus</i> Bulnheim	781



Taxon Name	Exsiccatae	Taxon Name	Exsiccatae
<i>Nitzschia bleischi</i> Janisch	1651	<i>Podosphenia remulus</i> Grunow	2000
<i>Nitzschia clausii</i> Hantzsch	944	<i>Rhoicosigma</i> Grunow	2000
<i>Nitzschia communis</i> Rabenhorst	949	<i>Rhoicosigma reichardtianum</i> Grunow	2000
<i>Nitzschia constricta</i> f. <i>minor</i> Rabenhorst	1503	<i>Rhoicosigma reichardtianum</i> var. <i>constrictum</i> Grunow	2000
<i>Nitzschia dubia</i> var. <i>minor</i> Grunow	1503	<i>Sceptroneis gemmata</i> Grunow	1998
<i>Nitzschia formica</i> Hantzsch	1403	<i>Schizostauron</i> Grunow	2000
<i>Nitzschia franconica</i> Reinsch	1891	<i>Schizostauron lindigianum</i> Grunow	2000
<i>Nitzschia franconica</i> var. <i>serpentina</i> Reinsch	1891	<i>Sphenella naviculoides</i> Hantzsch	1322
<i>Nitzschia gracilis</i> Hantzsch	946	<i>Stauroneis anceps</i> f. <i>gracilis</i> Rabenhorst	1268
<i>Nitzschia hantzschiana</i> Rabenhorst	943	<i>Stauroneis cohnii</i> Hilse	962
<i>Nitzschia incrustans</i> Grunow	1711 (1712)	<i>Stauroneis goeppertiana</i> Bleisch	1183
<i>Nitzschia kolaczekii</i> Grunow	2000	<i>Stauroneis janischii</i> Rabenhorst	848
<i>Nitzschia kurzeana</i> Rabenhorst	2312	<i>Stauroneis rotaeana</i> Rabenhorst	505
<i>Nitzschia kutzingiana</i> Hilse	1267	<i>Stauroneis undulata</i> Hilse	963
<i>Nitzschia media</i> Hantzsch	945	<i>Stauroptera truncata</i> Rabenhorst	812
<i>Nitzschia minuta</i> Bleisch	950	<i>Stephanogonia danica</i> Grunow	1998
<i>Nitzschia parvula</i> f. <i>elongata-gracilis</i> Hausknecht	2382	<i>Striatella intermedia</i> Grunow	2000
<i>Nitzschia perpusilla</i> Rabenhorst	1164	<i>Striatella lindigiana</i> Grunow	2000
<i>Nitzschia recta</i> Hantzsch	1283	<i>Surirella crumena</i> Brébisson ex Kutzing	1381
<i>Nitzschia schliephackeana</i> Grunow	1804	<i>Surirella diaphana</i> Bleisch	1489
<i>Nitzschia schweinfurthii</i> Grunow	1718	<i>Surirella gracilis</i> Grunow	1725
<i>Nitzschia stagnorum</i> Rabenhorst	625	<i>Surirella intermedia</i> Rabenhorst	642
<i>Nitzschia thermalis</i> var. <i>minor</i> Hilse	1266	<i>Surirella ovata</i> var. <i>intermedia</i> Rabenhorst	642
<i>Nitzschia tryblionella</i> Hantzsch	984	<i>Surirella ovata</i> var. <i>marina</i> Brébisson	2012
<i>Nitzschia tumida</i> Hantzsch	1114	<i>Surirella saxonica</i> Auerswald	1421
<i>Odontidium alpigenum</i> A.J. Kerner	1765	<i>Surirella suevica</i> Zeller	1045
<i>Odontidium hiemale</i> f. <i>rotundata</i> Rabenhorst	1084	<i>Surirella thuringiacea</i> Hantzsch	1208
<i>Odontidium rotundatum</i> Rabenhorst	1084	<i>Synedra aggregata</i> Brébisson ex Rabenhorst	687
<i>Peronia erinaceae</i> Brébisson & Arnott	2171	<i>Synedra amphirhynchus</i> var. <i>undulata</i> Rabenhorst	1323
<i>Pinnularia falaiseana</i> Krammer	611	<i>Synedra arcuata</i> Wigand	1046
<i>Pinnularia gibba</i> var. <i>curta</i> Bleisch	951	<i>Synedra bicurvata</i> Biene	1405
<i>Pinnularia hilseana</i> Janisch	953	<i>Synedra campyla</i> Hilse	1024
<i>Pinnularia medioconstricta</i> Bleisch	952	<i>Synedra cuneata</i> Grunow	2000
<i>Pinnularia ovalis</i> Hilse	1025	<i>Synedra formosa</i> Hantzsch	1403
<i>Pinnularia parvillissima</i> Krammer	1700	<i>Synedra frigida</i> Zeller	1561
<i>Pinnularia peracuminata</i> Krammer	1106	<i>Synedra gomphonema</i> Janisch & Rabenhorst	1481
<i>Pinnularia rabenhorstii</i> Hilse	842	<i>Synedra interrupta</i> Auerswald	403
<i>Pinnularia rupestris</i> Hantzsch	1203	<i>Synedra pulcherrima</i> Hantzsch	1403
<i>Pinnularia silesiaca</i> Bleisch in Fresenius	954	<i>Synedra splendens</i> var. <i>interrupta</i> Rabenhorst	403
<i>Pinnularia sudetica</i> Hilse	1023	<i>Synedra undosa</i> Grunow	2000
<i>Pinnularia viridis</i> var. <i>coerulescens</i> Hilse	1263	<i>Tessella hyalina</i> Janisch & Rabenhorst	1481
<i>Pinnularia viridula</i> (Kützing) Rabenhorst	682b	<i>Toxarium rostratum</i> Hantzsch	1403
<i>Plagiodiscus</i> Grunow & Eulenstein	2000	<i>Triceratium (orbiculatum</i> Shadbolt?) <i>elongatum</i> Grunow	2000
<i>Plagiodiscus nervatus</i> Grunow	2000	<i>Triceratium heibergianum</i> Grunow	1998
<i>Pleurosigma gracilentum</i> Rabenhorst	1066	<i>Triceratium jensenianum</i> Grunow	1998
<i>Pleurosigma scalproides</i> Rabenhorst	1101	<i>Triceratium sinense</i> Schwarz	2391
<i>Pleurostauron lineare</i> Hilse	1161	<i>Triceratium whampoense</i> Schwarz	2391
<i>Podosira kurzii</i> Zeller	2331		

(B) INVALID NAMES

Taxon Name	Exsiccatae	Taxon Name	Exsiccatae
<i>Achnanthidium lanceolatum</i> var. <i>major</i> Rabenhorst	2213	<i>Frustulia saxonica</i> f. <i>turfacea</i> Hilse	1954
<i>Amphora abbreviata</i> Bleisch in Rabenhorst	1489	<i>Gomphonema dichotomum</i> var. <i>affine</i> f. <i>minor</i> Grunow	1727
<i>Berkeleya dillwynii</i> var. <i>sericeum</i> Eiben	2234	<i>Melosira distans</i> f. <i>articulis-longioribus</i> Rabenhorst	1249
<i>Cocconeis grevillei</i> var. <i>minor</i> Grunow	2263	<i>Navicula calcuttensis</i> Grunow	2353
<i>Cocconeis parthenopaea</i> Pedicino	2223	<i>Nitzschia obtusa</i> var. <i>kurziana</i> Rabenhorst	2353
<i>Eunotia pectinalis</i> var. <i>undulata</i> f. <i>quinqueundulata</i> Grunow	1727	<i>Nitzschia palea</i> f. <i>curta</i> Grunow	2551
<i>Eunotia pectinalis</i> var. <i>undulata</i> f. <i>septemundulata</i> Grunow	1727	<i>Nitzschia rangoonensis</i> Grunow	2358
<i>Eunotia pectinalis</i> var. <i>undulata</i> f. <i>novemundulata</i> Grunow	1727	<i>Peronia erinacea</i> Brébisson & Arnott in Kitton	2171
<i>Eunotia pectinalis</i> var. <i>undulata</i> f. <i>quadriundulata</i> Grunow	1727	<i>Pinnularia gibba</i> f. <i>minor</i> Rabenhorst	1700
<i>Eunotia pectinalis</i> var. <i>undulata</i> f. <i>sexundulata</i> Grunow	1727	<i>Pleurosigma kurzianum</i> Grunow	2353
<i>Fragilaria hantzschiana</i> Gerstenberger	1041	<i>Synedra lunaris</i> var. <i>elongata</i> Brébisson	2025

### PART 3. TAXONOMIC STATUS OF NAMES PRESENTED AS NEW OR TYPIFIED IN RABENHORST EXSICCATAE

- Achnanthidium jackii* Rabenhorst 1861a, no. 1003. The name is also proposed in Rabenhorst 1864a, p. 106, but the description differs significantly from the exsiccatae that two separate species might be described under the same name from the same material.
- Achnanthidium jackii* Rabenhorst 1864a, p. 106. The name is also proposed in Rabenhorst 1861, no. 1003, but the description differs significantly from that of 1864 that two separate species might be described under the same name from the same material. Later homonym.
- Achnanthidium lanceolatum* var. *major* Rabenhorst 1870, no. 2213. Invalidly published name. No description.
- Achnanthidium thermale* Rabenhorst 1864a, p. 107.
- Amphiprora arenaria* Brébisson in Rabenhorst 1870, no. 2150.
- Amphitetras cruciata* Janisch & Rabenhorst 1863, p. 4; pl. 1, fig. 5.
- Amphitetras parvula* Janisch & Rabenhorst 1863, p. 4; pl. 1, fig. 4.
- Amphora abbreviata* Bleisch in Rabenhorst 1863c, no. 1489. Invalidly published name. No description.
- Amphora berggrenii* Cleve 1881, p. 4, pl. 4, fig. 3. Name (with no description) in Cleve & Möller 1878, no. 90, and in Rabenhorst 1878, no. 2560.
- Amphora bulnheimii* Rabenhorst 1866c, no. 1934.
- Amphora cymbelloides* Grunow 1867, p. 24.
- Amphora decussata* Grunow 1867, p. 23.
- Amphora hemisphaerica* Grunow 1867, p. 24.
- Amphora ovalis* f. *nana* Rabenhorst 1864a, p. 92. In index p. 327 as "var. *nana*".
- Amphora tumidula* Grunow in Rabenhorst 1864a, p. 175. Also described in no. 1716 (Rabenhorst 1864d).
- Asterionella bleakeleyi* var. *notata* Grunow 1867, p. 2.
- Bacillaria tropica* Grunow 1867, p. 19 (as *Bacillaria (paradoxa* var.?) *tropica*).
- Berkeleya dillwynii* var. *sericeum* Eiben in Rabenhorst 1870, no. 2234. Invalidly published name. No description.
- Berkeleya fusidium* Grunow 1867, p. 17.
- Campylodiscus punctatus* Bleisch 1860, p. 29; pl. 5, figs. 1–6.
- Campylodiscus rabenhorstianus* Janisch in Janisch & Rabenhorst 1863, p. 6; pl. 1, figs. 6–7. Illeg. Nom. superfluous (*C. ecclesianus* Greville and *C. fenestratus* Greville listed as synonyms).
- Campylodiscus rabenhorstii* Janisch ex Grunow 1862, p. 435. Also in Rabenhorst 1863a, p. 6, as *Campylodiscus rabenhorstianus* Janisch & Rabenhorst.
- Climacosphenia indica* Hantzsch in Rabenhorst 1863a, p. 18; pl. 5, fig. 1.
- Climacosphenia linearis* Janisch & Rabenhorst 1863, p. 6; pl. 2, fig. 2.
- Cocconeis flexella* Janisch & Rabenhorst 1863, p. 7; pl. 1, fig. 11.
- Cocconeis grevillei* var. *minor* Grunow ex Rabenhorst 1872, no. 2263. Invalidly published name. No description.
- Cocconeis heteroidea* Hantzsch in Rabenhorst 1863, p. 21; pl. 6 A, fig. 10.
- Cocconeis kirchenpauperiana* Janisch & Rabenhorst 1863, p. 7; pl. 1, fig. 9.
- Cocconeis parthenopoea* Pedicino in Rabenhorst 1870, no. 2223. Inv.
- Cocconeis pellucida* var. *minor* Grunow 1868, p. 13; pl. 1, fig. 7.
- Cocconeis pseudomarginata* var. *intermedia* Grunow 1868, p. 13; pl. 1, fig. 6.
- Cocconeis striolata* f. *substriolata* P. Reinsch in Rabenhorst 1866a, no. 1895. Description and illustration with exsiccatae. See also Reinsch 1866, p. 150.
- Cocconema nanum* Hantzsch in Rabenhorst 1862e, no. 1321.

*Cocconema pachycephalum* Rabenhorst 1861d, no. 1107, [4] figs.

*Cocconema variabile* Cramer in Rabenhorst 1862a, no. 1246.

*Cyclotella dubia* Hilse in Rabenhorst 1861a, no. 1022. Description also in Hilse 1860, p. 79.

*Cyclotella hilseana* Rabenhorst 1864a, p. 33. New name for *Cyclotella dubia* Hilse in Rabenhorst 1861.

*Cylindrotheca* Rabenhorst 1859a, no. 801.

*Cylindrotheca gerstenbergeri* Rabenhorst 1859a, no. 801.

*Cymatopleura marchica* Hermann in Rabenhorst 1868, no. 2061.

*Cymatopleura nobilis* Hantzsch 1860a, p. 36. Illustration in Rabenhorst 1861h, no. 1201.

*Cymbella cuspidata* f. *maxima* Rabenhorst 1864d, no. 1701.

*Cymbella cuspidata* f. *maxima* Rabenhorst 1868, p. 414 (as [*Cymbella cuspidata* var. *naviculiformis*] f. *maxima*). Name previously published as *Cymbella cuspidata* f. *maxima* in Rabenhorst 1864d, no. 1701.

*Cymbella cuspidata* var. *naviculiformis* (Auerswald in Rabenhorst) Rabenhorst 1864a, p. 78. Basionym: *Cymbella naviculiformis* Auerswald in Rabenhorst 1861b.

*Cymbella elegans* Cramer in Rabenhorst 1863a, p. 65.

*Cymbella hantzschiana* Krammer 2002, p. 47.

*Cymbella helvetica* f. *silesiaca* Rabenhorst 1857a, no. 604.

*Cymbella lunula* (Ehrenberg) Rabenhorst 1853, p. 23; pl. 7, fig. 11. Basionym: *Cocconema lunula* Ehrenberg 1843.

*Cymbella maculata* var. *major* Rabenhorst 1864a, p. 80. Rabenhorst cites as a synonym: "*Cymbella lunula* Hilse in Rabenhorst Alg. no. 1166". Previously identified by Rabenhorst as *Cymbella lunula* (Ehr.) Rabenhorst in no. 1166 (1861).

*Cymbella minuta* Hilse in Rabenhorst 1862b, no. 1261.

*Cymbella naviculiformis* Auerswald in Rabenhorst 1861b, no. 1065. Invalidly published name. No description.

*Cymbella naviculiformis* Auerswald ex Heiberg 1863, p. 108; pl. 1, fig. 2.

*Cymbella silesiaca* Bleisch in Rabenhorst 1865c, no. 1802.

*Cymbella variabilis* Wartmann in Rabenhorst 1859a, no. 803.

*Cymbella vulgata* Krammer 2002, p. 55.

*Denticella ventricosa* Janisch & Rabenhorst 1863, p. 8; pl. 2, fig. 11.

*Denticula elegans* var. *valida* Pedicino 1867, p. 7; pl. 1, figs. 42–45.

*Denticula quadrata* Kuntze in Rabenhorst 1866c, no. 1933.

*Desmogonium rabenhorstianum* Grunow 1865, p. 6; pl. 1, fig. 1.

*Diatoma elongatum* var. *abbreviatum* Rabenhorst 1864a, p. 122. (= *Diatoma elongatum* v. 'gamma' Smith 1856).

*Diatoma gracillimum* Hantzsch in Rabenhorst 1861d, no. 1104b + figs. a–b ('*gracillimum*')

*Encyonema auerswaldii* Rabenhorst 1853, p. 24; pl. 7, *Encyonema* : fig. 2.

*Encyonema gerstenbergeri* Grunow 1865, p. 9; pl. 1, fig. 11.

*Encyonema maximum* Wartmann ex Rabenhorst 1862a, no. 1248.

*Encyonema prostratum* f. *helvetica-robustior* Rabenhorst 1860b, no. 958.

*Epithemia goeppertiana* Hilse 1860, p. 79 (Göppertiana). Also in Rabenhorst 1861, no. 1021.

*Epithemia göppertiana* Hilse in Rabenhorst 1861, no. 1021.

*Epithemia intermedia* Hilse 1860, p. 76. Also described in exsiccatae no. 1026a (Rabenhorst 1861).

*Epithemia intermedia* Hilse in Rabenhorst 1861, no. 1026a.

*Epithemia intermedia* Wartmann in Rabenhorst 1861c, no. 1089. Error cit. for *Epithemia zebra* var. *intermedia* Wartmann in Rabenhorst.

*Epithemia minuta* Hantzsch in Rabenhorst 1863d, no. 1501.



*Epithemia rabenhorstii* Wartmann in Rabenhorst 1861c, no. 1088.

*Epithemia zebra* var. *intermedia* Wartmann in Rabenhorst 1861c, no. 1089.

*Eunotia camelus* var. *denticulata* Grunow 1865, p. 4; pl. 1, fig. 6d. Listed in Van Landingham's *Catalogue* (1969) as a new combination of *Himanthidium denticulatum* Brébisson in Kützing. Treated here as the name of a new species because Grunow expressed doubt (query) regarding the synonymy.

*Eunotia camelus* var. *didymodon* Grunow 1865, p. 4; pl. 1, fig. 6c (as *Eunotia camelus* var. 'beta' *didymodon*).

*Eunotia camelus* var. *genuina* Grunow 1865, p. 4; pl. 1, figs. 6a–b (as *Eunotia camelus* Ehrenb. var. 'alpha' *genuina*).

*Eunotia formica* var. *bigibba* Grunow 1865, p. 3; pl. 1, figs. 2f–g (as *Eunotia formica* var. 'delta' *bigibba*).

*Eunotia formica* var. *elongata* Grunow 1865, p. 3; pl. 1, figs. 2a–b (as *Eunotia formica* Ehr. var. 'alpha' *elongata*).

*Eunotia formica* var. *genuina* Grunow 1865, p. 3; pl. 1, figs. 2c–d (as *Eunotia formica* var. 'beta' *genuina*).

*Eunotia formica* var. *intermedia* Grunow 1865, p. 3; pl. 1, fig. 2e (as *Eunotia formica* var. 'gamma' *intermedia*).

*Eunotia indica* Grunow 1865, p. 5; pl. 1, figs. 7a–b.

*Eunotia indica* var. *ventralis* Grunow 1865, p. 5; pl. 1, fig. 7c (as *Eunotia indica* var. 'beta' *ventralis*).

*Eunotia kurzeana* Grunow in Möller 1881, Typ. pl. 1.2.2.

*Eunotia kurziana* Grunow in Rabenhorst 1873, no. 2357. Invalidly published name. No description. Probable orthographic variant of *Eunotia kurzeana* Grunow.

*Eunotia kurziana* Grunow in Cleve & Möller 1878, no. 129. Invalidly published name. No description.

*Eunotia major* var. *octoundulata* Grunow 1865, p. 5; pl. 1, fig. 8. Illustrated as *Eunotia major* var. *undulata*.

*Eunotia major* var. *sexundulata* Grunow 1865, p. 5. Invalidly published name. No description. See *Eunotia major* var. *undulata* Grunow 1865.

*Eunotia major* var. *undulata* Grunow 1865, p. 16; pl. 1, fig. 8, p. 5. Described in text p. 5 as var. *sexundulata* and var. *octoundulata*.

*Eunotia minuta* Hilse in Rabenhorst 1861f, no. 1167.

*Eunotia minuta* Hilse 1860, p. 79. See also Rabenhorst 1861, no. 1167.

*Eunotia pectinalis* f. *biundulata* Grunow 1865, p. 4; pl. 1, fig. 5a (as *Eunotia pectinalis* var. *undulata* f. *biundulata*). Invalidly published name. No description.

*Eunotia pectinalis* f. *octoundulata* Grunow 1865, p. 4; pl. 1, fig. 5c (as *Eunotia pectinalis* var. *undulata* f. *octoundulata*). Invalidly published name. No description.

*Eunotia pectinalis* f. *quadriundulata* Grunow 1865, p. 4; pl. 1 (as *Eunotia pectinalis* var. *undulata* f. *quadriundulata*). Invalidly published name. No description.

*Eunotia pectinalis* f. *quinqueundulata* Grunow 1865, p. 4 (as *Eunotia pectinalis* var. *undulata* f. *sexundulata*). Invalidly published name. No description.

*Eunotia pectinalis* f. *septemundulata* Grunow 1865, p. 4 (as *Eunotia pectinalis* var. *undulata* f. *septemundulata*). Invalidly published name. No description.

*Eunotia pectinalis* f. *sexundulata* Grunow 1865, p. 4 (as *Eunotia pectinalis* var. *undulata* f. *sexundulata*). Invalidly published name. No description.

*Eunotia pectinalis* var. *triundulata* Grunow 1865, p. 4. Invalidly published name. No description.

*Eunotia ventricosa* var. *elongata* Grunow 1865, p. 4; pl. 1, fig. 4.

*Eupodiscus minutus* Hantzsch in Rabenhorst 1863a, p. 21; pl. 6A, fig. 9.

*Eupodiscus roperi* Brébisson in Rabenhorst 1867, no. 2005 ('*roperii*'). New name for *Coscinodiscus ovalis* Roper 1858 (priority for *Eupodiscus ovalis* Norman 1861).

*Eupodiscus roperi* Brébisson 1870, p. 41 ('*roperii*'). Previously published in Rabenhorst 1867, no. 2005.

*Falcatella zelleri* Rabenhorst 1857a, no. 561.

*Falcatella zelleri* Rabenhorst 1864a, p. 139. Inv. Cited pro syn. *Synedra zelleri* Rabenhorst.

*Fragilaria hantzschiana* Gerstenberger in Rabenhorst 1861b, no. 1041. Inv. In syn. *Fragilaria mesolepta* Rabenhorst.

*Fragilaria mesolepta* Rabenhorst 1861b, no. 1041. Also in Rabenhorst 1863a, p. 30.

*Fragilaria undulata* Cramer 1863, p. 65; pl. 12, fig. 7.

*Frustulia saxonica* f. *torfacea* (A. Braun ex Rabenhorst) Rabenhorst 1864a, p. 227 (as var. in index p. 333).  
Basionym: *Frustulia torfacea* A. Braun ex Rabenhorst 1853.

*Frustulia saxonica* f. *torfacea* Hilse ex Rabenhorst 1867, no. 1954. Invalidly published name. No description..  
Perhaps this is just a citation error for *Frustulia saxonica* var. *torfacea* (Braun ex Rabenhorst) Rabenhorst 1864.

*Frustulia torfacea* A. Braun ex Rabenhorst 1853, p. 50; pl. 7, *Frustulia*: fig. 2. Epithet spelled “*torphacea*” in *exsiccatae* no. 761.

*Gomphogramma rupestre* (Kützing) Braun in Rabenhorst 1853, p. 33, 67; pl. 9, fig. 1. Basionym: *Denticula thermalis* var. *rupestris* Kützing 1849.

*Gomphonema capitatum* var. *gracile* Rabenhorst 1858, no. 743.

*Gomphonema dichotomum* f. *minor* Grunow 1865, p. 10 (as *Gomphonema dichotomum* var. *affine* f. *minor*).  
Inv. Nomen nudum.

*Gomphonema turris* var. *apiculatum* Grunow 1865, p. 10; pl. 2, fig. 12.

*Heliopelta ehrenbergii* Eulenstein ex Rabenhorst 1865c, no. 1806. Illeg. *Nomen novum*. *H. metii* Ehrenb., *H. leeuwenhockii* Ehrenb. and *H. eulerei* Ehrenb. given as synonyms.

*Himantidium dilatatum* Wigand 1860, p. 43; pl. 7, fig. 9.

*Himantidium striatum* Wigand 1860, p. 43; pl. 7, fig. 10–12.

*Homoeocladia bulnheimiana* Rabenhorst 1862d, no. 1301. Also described in Rabenhorst 1863a, p. 617 and Rabenhorst 1864a, p. 167.

*Homoeocladia dufourii* De Notaris in De Notaris & Baglietto 1871, Erbar. Critt. it. No. 764.

*Isthmia lindigiana* Grunow & Eulenstein in Grunow 1867, p. 29.

*Licmophora divisa* f. *japonica* Rabenhorst 1874, no. 2380.

*Licmophora gracilis* f. *borealis* (Kützing) Grunow 1867, p. 35. Basionym: *Rhipidophora borealis* Kützing 1844.

*Licmophora gracilis* f. *constricta* Grunow 1867, p. 34.

*Mastogloia interrupta* Hantzsch in Rabenhorst 1863a, p. 20; pl. 6A, figs. 5a–b.

*Melosira distans* f. *articulis-longioribus* Rabenhorst 1862a, no. 1249. Invalidly published name. No illustration or description.

*Melosira pfaffiana* Reinsch in Rabenhorst 1866b, no. 1912. Also in Reinsch 1866.

*Melosira roeseana* Rabenhorst 1853, p. 13; pl. 10, supplemente: fig. 5.

*Melosira roeseana* Rabenhorst 1854, no. 383. Description previously published.

*Navicula bleischiana* Janisch & Rabenhorst 1863, p. 9; pl. 2, fig. 10.

*Navicula calcuttensis* Grunow in Rabenhorst 1873, no. 2353. Invalidly published name. No description.

*Navicula humerosa* Brébisson ex W. Smith 1856, p. 93.

*Navicula janischiana* Rabenhorst in Janisch & Rabenhorst 1862, p. 10; pl. 2, fig. 15.

*Navicula lobata* Schwartz in Rabenhorst 1877, no. 2481. Description in Latin and illustration are provided.

*Navicula macrogongyla* Rabenhorst 1860a, p. 40; pl. 6, fig. 10.

*Navicula major* var. *crassa* Brébisson in Rabenhorst 1858a, no. 683. Invalidly published name. No description. Name of taxon validly published as *Pinnularia major* var. *crassa* Rabenhorst 1864a, p. 210.

*Navicula marina* Janisch & Rabenhorst 1863, p. 10; pl. 2, fig. 16. Illeg. Non Ralfs 1861.

*Navicula nodosa* f. *curta* Rabenhorst 1864a, p. 207. As ‘var.’ in index p. 338. Syn: *Navicula quinquenodis* Grunow 1860. New name for Grunow’s taxon.

*Navicula reinickeana* Rabenhorst 1859a, no. 802. Brief description provided. Description also in Rabenhorst 1863a, p. 35.

*Navicula reticulata* Grunow 1867, p. 26.

*Navicula rotundata* Hantzsch in Rabenhorst 1862c, no. 1283b.

*Navicula seminumum* var. *fragilarioides* Grunow in Van Heurck 1880, pl. 14, fig. 10.

*Navicula splendens* Schwartz in Rabenhorst 1877, no. 2483. Illustration with no. 2481.

*Navicula triundulata* Grunow 1867, p. 27.

*Nitzschia affinis* f. *major* Grunow 1867, p. 18.

*Nitzschia arcus* Bulnheim 1859, p. 22; pl. 2, fig. 1.

*Nitzschia bleischii* Janisch in Bleisch 1863, p. 78.

*Nitzschia bleischii* Janisch in Rabenhorst 1864c, No. 1651.

*Nitzschia clausii* Hantzsch 1860b, p. 40; pl. 6, fig. 7. Illustration only. Brief description with exsiccatae no. 944 (1860). Description in Grunow 1862, p. 573, 559.

*Nitzschia communis* Rabenhorst 1860b, no. 949. Reference to a published illustration (*Hedwigia* II, pl. 6, fig. 3) is given. Described in Grunow 1862, p. 561, 578 and Rabenhorst 1864a, p. 159.

*Nitzschia constricta* f. *minor* Rabenhorst 1863a, p. 153.

*Nitzschia dubia* var. *minor* Grunow 1862, p. 568; pl. 28/12, figs. 24a–b.

*Nitzschia formica* Hantzsch in Rabenhorst 1863a, p. 21; pl. 6 A, fig. 8.

*Nitzschia franconica* Reinsch 1866, p. 26; pl. 1, figs. 1a, c–e. See also Rabenhorst 1866a, no. 1891.

*Nitzschia franconica* var. *serpentina* Reinsch 1866, p. 27; pl. 1, figs. 1b–c. See also Rabenhorst 1866a, no. 1891.

*Nitzschia gracilis* Hantzsch 1860b, p. 40; pl. 6, fig. 8. Illustration only. Brief description in exsiccatae no. 946. Description in Grunow 1862, p. 560, 575.

*Nitzschia hantzschiana* Rabenhorst 1860a, p. 40; pl. 6, fig. 6. Brief description in exsiccatae no. 943. Description in Grunow 1862, p. 576.

*Nitzschia hantzschiana* Rabenhorst in Grunow 1862, p. 576.

*Nitzschia incrustans* Grunow 1862, p. 566; pl. 28/12, figs. 21a–f.

*Nitzschia kolaczekii* Grunow 1867, p. 18. Spelled *kolaizeckii* in 1877.

*Nitzschia kolaizeckii* Grunow 1877, p. 173. Orth. var. of *Nitzschia kolaczekii* Grunow 1867.

*Nitzschia kuetzingiana* Hilse in Rabenhorst 1862b, no. 1267.

*Nitzschia kuetzingii* Rabenhorst 1864a, p. 160 [ref. 775]. Valid name for *Nitzschia kuetzingiana* Hilse in Rabenhorst 1862b, no. 1267.

*Nitzschia kurzeana* Rabenhorst 1873, no. 2312.

*Nitzschia media* Hantzsch 1860b, p. 40; pl. 6, fig. 9. Illustration only. Brief description in exsiccatae no. 945. Description in Grunow 1862, p. 576.

*Nitzschia minuta* Bleisch in Rabenhorst 1860b, No. 950. Description also in Bleisch 1863, p. 78 and Grunow 1862, p. 578.

*Nitzschia minuta* Bleisch 1863, p. 78.

*Nitzschia obtusa* var. *kurziana* Rabenhorst 1873, no. 2353. Invalidly published name. No description.

*Nitzschia obtusa* var. *schweinfurthii* (Grunow) Grunow in Cleve & Grunow 1880, p. 92. Basionym: *Nitzschia schweinfurthii* Grunow in Rabenhorst 1864.

*Nitzschia palea* f. *curta* Grunow ex Rabenhorst 1878, no. 2551. Invalidly published name. No description.

*Nitzschia parvula* f. *elongata-gracilis* Hausknecht in Rabenhorst 1874, no. 2382 ('*elongata gracilis*').

*Nitzschia perpusilla* Rabenhorst 1861f, no. 1164. Also in Rabenhorst 1864a, p. 159, and Hilse 1863, p. 67.

*Nitzschia perpusilla* Rabenhorst in Hilse 1863, p. 67. Previously validly published in Rabenhorst 1861f.

*Nitzschia rangoonensis* Grunow ex Rabenhorst 1873, no. 2358. Invalidly published name. No description.

*Nitzschia recta* Hantzsch ex Rabenhorst 1862c, No. 1283.

*Nitzschia schliephackeana* Grunow ex Rabenhorst 1864a, p. 324.

*Nitzschia schweinfurthii* Grunow in Rabenhorst 1864a, p. 175.

*Nitzschia stagnorum* Rabenhorst 1857a, no. 625.

*Nitzschia thermalis* var. *minor* Hilse in Rabenhorst 1862b, no. 1266. Name also in Hilse 1863, p. 67.

*Nitzschia thermalis* var. *stagnorum* (Rabenhorst) Rabenhorst 1864a, p. 154. Basionym: *Nitzschia stagnorum* Rabenhorst 1857.



- Nitzschia tryblionella* Hantzsch in Rabenhorst 1860c, No. 984. New name for *Tryblionella gracilis* Smith 1853 (priority for *Nitzschia gracilis* Hantzsch 1860).
- Nitzschia tumida* Hantzsch in Rabenhorst 1861e, No. 1114. Illustration only. Description in Rabenhorst 1864a, p. 153.
- Odontidium alpigenum* Kerner ex Rabenhorst 1865b, no. 1765. First appeared as *nomen nudum* in *Hedwigia* 4, p. 56 (1864).
- Odontidium hiemale* (hyemale) f. *rotundata* (Rabenhorst) Rabenhorst 1864a, p. 116. Basionym: *Odontidium rotundatum* Rabenhorst 1853.
- Odontidium rotundatum* Rabenhorst 1853, p. 34; pl. 2, fig. 4 c. Illeg. Non (Ehrenberg) Kützing 1849. The epithet appears in Rabenhorst 1853, on p. 34 (under *O. hiemale*) with an unclear status (new species of *Odontidium* or new subdivision of *O. hiemale*?). Nevertheless, the name *Odontidium rotundatum* is definitely validly published with the illustration and plate caption.
- Peronia erinacea* Brébisson & Arnott ex Kitton 1868, p. 16. Illeg. *Gomphonema fibula* Brébisson ex Kützing 1849 cited as synonym. Name illegitimate, correct names for this taxon: *Gomphonema fibula* Bréb. ex Kützing, *Peronia fibula* (Bréb. ex Kützing) Ross.
- Pinnularia falaiseana* Krammer 1992, p. 113–114, 172; pl. 41, figs. 5–8, 10–11.
- Pinnularia gibba* var. *curta* Bleisch 1860, no. 951 (as *Pinnularia gibba* forma *curta*, varietas nova). Description also in Rabenhorst 1863b, p. 39 (as *Pinnularia gibba* b. *curta*).
- Pinnularia gibba* f. *minor* Rabenhorst 1864b, no. 1700. Invalidly published name. No description.
- Pinnularia hilseana* Janisch in Rabenhorst 1860b, no. 953. See also Hilse 1860, p. 82.
- Pinnularia major* var. *crassa* Rabenhorst 1864a, p. 210.
- Pinnularia medioconstricta* Rabenhorst 1860b, no. 952 ('*medio constricta*'). See also Bleisch 1863, p. 81.
- Pinnularia ovalis* Hilse 1860, p. 82.
- Pinnularia ovalis* Hilse in Rabenhorst 1861b, no. 1025.
- Pinnularia parvillissima* Krammer 2000, p. 95.
- Pinnularia peracuminata* Krammer 2000, p. 157.
- Pinnularia rabenhorstii* Hilse 1860, p. 82.
- Pinnularia rupestris* Hantzsch in Rabenhorst 1861h, no. 1203.
- Pinnularia silesiaca* Bleisch in Fresenius 1862, p. 68; pl. 4, figs. 25–29.
- Pinnularia silesiaca* Bleisch in Rabenhorst 1863a, p. 38. The *exsiccatae* (no. 954) does not provide a description, but refers to an illustration (*Hedwigia* II, pl. 4 figs. 3–4). See also Bleisch in Fresenius 1862.
- Pinnularia sudetica* Hilse 1860, p. 82.
- Pinnularia sudetica* Hilse in Rabenhorst 1861, no. 1023.
- Pinnularia viridis* var. *coerulescens* Hilse in Rabenhorst 1862b, no. 1263. Also in Hilse 1863, p. 68.
- Pinnularia viridula* (Kützing) Rabenhorst 1853, p. 43, 69; pl. 6, fig. 39. Basionym: *Frustulia viridula* Kützing 1833 (1834).
- Plagiodiscus* Grunow & Eulenstein in Grunow 1867, p. 8.
- Plagiodiscus nervatus* Grunow 1867, p. 8.
- Pleurosigma gracilentum* Rabenhorst 1861b, no. 1066. Also in Rabenhorst 1863a, p. 617 and Rabenhorst 1864a, p. 240.
- Pleurosigma kurzianum* Grunow ex Rabenhorst 1873, no. 2353. Invalidly published name. No description.
- Pleurosigma scalproides* Rabenhorst 1861d, no. 1101 + fig. Also in Rabenhorst 1863a, p. 41, and Rabenhorst 1864a.
- Pleurostaurum acutum* (W. Smith) Rabenhorst 1859c, p. 17; pl. 1, fig. B, pl. 2, fig. F. Basionym: *Stauroneis acuta* W. Smith 1853.
- Pleurostaurum lineare* Hilse 1860, p. 83. Valid as the name of a new taxon. Could also be treated as a new combination of *Stauroneis linearis* Ehrenberg.
- Pleurostaurum lineare* Rabenhorst 1861f, no. 1161. Valid as the name of a new taxon. Could also be treated as a new combination of *Stauroneis linearis* Ehrenberg.

*Pleurostaurum lineare* (Ehrenberg) Rabenhorst 1863a, p. 43. Basionym: *Stauroneis linearis* Ehrenberg 1843.

*Podosira kurzii* Zeller 1873, p. 175 (= p. 2).

*Podosphenia remulus* Grunow 1867, p. 2.

*Rhoicosigma* Grunow 1867, p. 19.

*Rhoicosigma reichardtianum* Grunow 1867, p. 19.

*Rhoicosigma reichardtii* Grunow 1877, p. 181. Orth. var. of *Rhoicosigma reichardtianum* Grunow 1867.

*Rhoicosigma reichardtii* var. *constrictum* Grunow 1877, p. 181.

*Sceptroneis gemmata* Grunow 1866, p. 146.

*Schizostauron* Grunow 1867, p. 28.

*Schizostauron lindigianum* Grunow 1867, p. 28.

*Schizostauron lindigii* Grunow 1877, p. 181; pl. 195, fig. 17. Orth. var. for *Schizostauron lindigianum* Grunow 1867.

*Sphenella naviculoides* Hantzsch in Rabenhorst 1862, no. 1322.

*Stauroneis anceps* f. *gracilis* Rabenhorst 1864a, p. 247.

*Stauroneis cohnii* Hilse in Rabenhorst 1860b, no. 962.

*Stauroneis goeppertiana* Bleisch ex Rabenhorst 1861g, No. 1183. Also in Bleisch 1863, p. 81.

*Stauroneis janischii* Rabenhorst 1859b, No. 848f, fig. f.

*Stauroneis rotaeana* Rabenhorst 1856, p. 103; pl. 13, fig. 7. Illustration only. For descriptions see Grunow 1860, p. 565 and Rabenhorst 1864a, p. 249. Latin description also included in exsiccatae no. 505 (1856).

*Stauroneis undulata* Hilse 1860, p. 83. Brief description also in the exsiccatae Rabenhorst 1860b, no. 963.

*Stauoptera truncata* Rabenhorst 1853, p. 49; pl. 9, fig. 12.

*Stephanogonia danica* Grunow 1866, p. 146.

*Striatella intermedia* Grunow 1867, p. 6.

*Striatella lindigiana* Grunow 1867, p. 6.

*Surirella crumena* Brébisson ex Kützing 1849, p. 38. In same publication, cited pro syn. *Cyclotella meneghiniana* 'beta' major (p. 19).

*Surirella diaphana* Bleisch in Rabenhorst 1863c, no. 1489. Also in Bleisch 1863, p. 78.

*Surirella gracilis* (W. Smith) Grunow 1862, p. 144; pl. 7/10, fig. 11. Basionym: *Tryblionella gracilis* W. Smith 1853.

*Surirella intermedia* Rabenhorst 1857b, no. 642. Brief description provided. Described in Latin in Rabenhorst 1864a, p. 57 as *Surirella ovata* b. *intermedia*.

*Surirella ovata* var. *intermedia* (Rabenhorst) Rabenhorst 1864a, p. 57, 345 (as *Surirella ovata* b. *intermedia* on p. 57, as var. *intermedia* on p. 345). Basionym: *Surirella intermedia* Rabenhorst 1857. New combination if basionym is valid; valid name of a new taxon otherwise.

*Surirella ovata* var. *marina* Brébisson in Rabenhorst 1867, no. 2012.

*Surirella saxonica* Auerswald in Rabenhorst 1863b, no. 1421. Also described in Rabenhorst 1864a, p. 53.

*Surirella suevica* Zeller in Rabenhorst 1861b, no. 1045.

*Surirella suevica* Zeller ex Grunow in Schmidt et al. 1875, pl. 23, figs. 56–60. Name already published in Rabenhorst 1861b, no. 1045.

*Surirella thuringiaceae* Hantzsch in Rabenhorst 1861h, no. 1208.

*Synedra aggregata* Brébisson ex Rabenhorst 1858a, No. 687.

*Synedra amphirhynchus* var. *undulata* Rabenhorst 1862a, no. 1323. A diagnosis is provided with the exsiccatae. Also Rabenhorst 1864a, p. 134.

*Synedra arcuata* Wigand 1860, p. 44; pl. 7, fig. 15.

- Synedra bicurvata* Biene ex Rabenhorst 1863b, No. 1405. No description in exsiccatae, but reference to an illustration (*Hedwigia* II, pl. 2, fig. 1). Described in Rabenhorst 1864a, p. 120.
- Synedra bicurvata* Biene ex Rabenhorst 1864a, p. 120.
- Synedra campyla* Hilse 1860, p. 84.
- Synedra campyla* Hilse in Rabenhorst 1861, no. 1024a.
- Synedra cuneata* Grunow 1867, p. 5. Illeg. Non Ehrenberg 1834.
- Synedra formosa* Hantzsch in Rabenhorst 1863a, p. 19; pl. 5, fig. 3.
- Synedra frigida* Zeller in Rabenhorst 1863e, no. 1561.
- Synedra gomphonema* Janisch & Rabenhorst 1863, p. 13; pl. 2, fig. 6.
- Synedra interrupta* Auerswald in Rabenhorst 1855, No. 403.
- Synedra lunaris* var. *elongata purissima* A. de Brébisson ex Rabenhorst 1867, no. 2025. Invalidly published name. No description.
- Synedra pulcherrima* Hantzsch in Rabenhorst 1863a, p. 19; pl. 5, fig. 2.
- Synedra splendens* var. *interrupta* (Auerswald in Rabenhorst) Rabenhorst 1864a, p. 134. Basionym: *Synedra interrupta* Auerswald in Rabenhorst 1855.
- Synedra undosa* Grunow 1867, p. 4.
- Synedra zelleri* Rabenhorst 1864a, p. 139. New combination of *Falcatella zelleri*?
- Tessella (Tessela) hyalina* Janisch & Rabenhorst 1863, p. 13; pl. 2, fig. 13.
- Toxarium rostratum* Hantzsch 1863, p. 19; pl. 5, fig. 4.
- Triceratium elongatum* Grunow 1867, p. 31 (as *Triceratium (orbiculatum* var?) *elongatum*).
- Triceratium heibergianum* Grunow 1866, p. 145.
- Triceratium jensenianum* Grunow 1866, p. 145.
- Triceratium sinense* Schwarz 1874, p. 163.
- Triceratium whampoense* Schwarz 1874, p. 163.

#### ACKNOWLEDGMENTS

I want to take this opportunity to thank Dr. Elizabeth Foutanier for her extensive work on the taxonomic status of taxa considered herein; also, Dr. Michele L. Aldrich who perused the entire manuscript in its penultimate typeset format. With a keen editorial eye, she uncovered both textual and formatting inconsistencies that I had missed, thus giving me an opportunity to make changes before committing the whole to print. Drs. Robert Edgar and David Williams reviewed the paper in its penultimate form and offered many suggestions for its improvement. I am indebted to both for the care they took in their reviews. And, last but not least, thanks are due Dr. J. Thomas Dutro, Jr., U.S. Geological Survey [ret.], National Museum of Natural History, Washington, D.C., who generously assisted in arranging with the Department of Botany at the Museum to make available their copy of Rabenhorst's 1864 edition of *Flora Europaea Algarum* from which I secured the copy of Rabenhorst's portrait that is reproduced here. To all of the above, my sincere thanks with the caveat that I alone take responsibility for any errors of commission or omission that still exist.

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## A SEM Study of the Diatom Genus *Porodiscus* Greville; Morphology of the Species and Comparison with Related Genera

N.I. Strelnikova<sup>1</sup>, E. Fourtanier<sup>2</sup>, J.P. Kociolek<sup>2</sup>, and J.A. Barron<sup>3</sup>

<sup>1</sup> Department of Botany, Biological Faculty, St. Petersburg State University, Universitetskaya Emb. 7/9, St. Petersburg 199034, Russia; Email: diatomspb@mail.ru. <sup>2</sup> Diatom Collection, California Academy of Sciences, 875 Howard Street, San Francisco, California 94103, USA; Email: efourtanier@calacademy.org, pkociolek@calacademy.org. <sup>3</sup> United States Geological Survey, MS910, 345 Middlefield Rd, Menlo Park, California 94025, USA; Email: jbarron@usgs.gov.

We carried out SEM studies on the poorly known middle Eocene marine diatom genus *Porodiscus* Greville. Species examined include, *Porodiscus splendidus* Greville, *P. nitidus* Greville, *P. conicus* Greville, *P. oblongus* Greville. Selected species in the related genera *Coscinodiscus* Ehrenberg, *Craspedodiscus* Ehrenberg and *Annellus* Tempère are also considered. Two new combinations, *Porodiscus splendidus* var. *excentricus* (Olshtinskaya) Olshtinskaya n. comb. and *Porodiscus splendidus* var. *corniger* (Brun) Fourtanier n. comb. are proposed, and we designate *Porodiscus nitidus* Greville as the lectotype of *Porodiscus* Greville. *Porodiscus* resembles both *Coscinodiscus* and *Craspedodiscus* in the presence of locular areolae, which possess external cribra and internal foramina, and the presence of marginal rimoportulae. *Porodiscus* has unique characters, however, such as spines occurring in some taxa, which are not present in *Coscinodiscus* or *Craspedodiscus*. *Porodiscus* possesses a distinctive central cavity (or “sack”), similar to that of *Craspedodiscus*; however, in *Porodiscus*, the central cavity is very steep (tube-like) and well defined, being bordered by a hyaline rim. *Craspedodiscus* species usually do not have such hyaline rim (except for some tropical Miocene forms of *Craspedodiscus coscinodiscus*) and lack a well-defined central depression.

*Porodiscus* Greville 1863 is a small, poorly known genus of fossil centric marine diatoms closely allied to *Coscinodiscus* Ehrenberg from which it differs by the presence of a deep concavity at the center of the valve. The genus has received little attention by taxonomists, and the only SEM observations to date are those of Sims (1989) on a species identified as *Porodiscus nitidus* var. *armatus* Ratray from Joe’s River, Barbados. Sims’ specimens were not sufficiently well preserved to observe the shape of the rimoportulae and the nature of the cribrum. Her observations, however, confirm the affinity of *Porodiscus* with *Coscinodiscus*, which was first noted by Greville (1863). We present here new information on the morphology of this intriguing genus based on detailed SEM observations and reexamination of Greville’s original slides.

Our interest in the genus first arose after the observation under SEM of *Porodiscus splendidus* (?) from a sample taken from DSDP Site 206, Core 16, Section 5 (Tasman Sea), a specimen with spines. A review of the literature indicated that *P. splendidus* Greville was the most cited and the most widely distributed species of *Porodiscus*. Illustrations of the reported specimens, however, showed both specimens with spines (Gombos 1983) and specimens without spines (Fenner 1985). This prompted us to reexamine the type material of Greville for that species and to consider the other species in the genus.

## HISTORICAL PERSPECTIVE

Greville (1863:63) described the genus *Porodiscus* from samples prepared by Johnson from the sediments of the Cambridge Estate in Barbados (middle-late Eocene according to the stratigraphic scheme of Mitchell-Thome 1979). He originally included five species: *P. nitidus*, *P. elegans*, *P. major*, *P. conicus* and *P. oblongus* (*P. ovalis* in plate caption), but did not designate a generic type. Subsequently, Greville (1865:46) described *Porodiscus splendidus* from the sediments of the Springfield Estate, Barbados, whose precise stratigraphic position is not known. Greville (1865) noted that *P. splendidus* was not found in the Cambridge Estate sediments.

Greville (1863) described the genus in these words: "Frustules free, disciform, composed of two discs, united by an intermediate, ring-like zone; discs very convex, minutely radiato-cellulate or punctate, with a conspicuous central pseudo-opening." Greville continued: "This genus is evidently closely allied to *Coscinodiscus*, differing chiefly in the remarkable pore-like pseudo-opening, which is not a mere blank circular space produced by the absence of cellulation at the apex, but a well-defined, concave, apparent orifice, provided with a thickened margin." Greville added that "all the species described from Barbados had very convex valves, and puncta [areolae] arranged in radial rows. In nearly all the species certain of the radial rows start from the margin and continue to the valve apex, dividing the valve into perceptible sections [fascicles]. Surface is either plane or armed with variously arranged minute spines." The types of Greville's *Porodiscus* are illustrated by Williams (1988:44–45, pl. 52, figs. 1–9, pl. 53, fig. 5).

Castracane (1886) described *P. stolterfothii*, which he considered an extant species, from the tropical area of the Pacific Ocean. Grove and Sturt (1887) described two other species of *Porodiscus*: *P. hirsutus* and *P. interruptus*, from Oamaru (New Zealand, upper Eocene). Rattray (1890) described *Porodiscus spiniferus*, *P. splendidus* var. *marginata*, *P. major* var. *densa*, and *P. nitidus* var. *armata* from Barbados. *Porodiscus corniger* Brun (1896) was also described from Barbados from the Chimborazo sediments (unknown age) and Mount Hillaby (late Eocene). *Porodiscus calyciflos* Tempère and Brun in Brun and Tempère, 1889, is known from a Neogene limestone of Yedo, Yedo Bay, Japan, and is also known as living in the Sandwich Islands (Brun and Tempère 1889). Prema and Desikachary (1989) described *Porodiscus minor* and *Porodiscus venkataraminii* from the Oligocene of the Indian Ocean.

The generic placement of these species has been questioned. Mann (1907:237), noted that *P. calyciflos*, *P. interruptus*, *P. hirsutus* (which he placed in synonymy) have nothing in common with Greville's genus. Jousé in Proschkina-Lavrenko (1949:33) created the illegitimate name *Pseudopodosira pileiformis* as a synonym of *P. calyciflos*. Various authors (e.g., Gombos 1982; Prema and Desikachary 1989) have also recognized the similarity of *Porodiscus* with *Craspedodiscus* Ehrenberg, a closely related genus with a central depression. Grunow 1881 in Schmidt (pl. 66, figs. 7–9) transferred *Porodiscus oblongus* Grev. to *Craspedodiscus oblongus*. Gombos (1982:232) transferred *Porodiscus splendidus* Grev. to *Craspedodiscus splendidus*.

Based on our observations of original illustrations and descriptions, we recognize that the genus *Porodiscus* in Greville's original sense currently contains the species of Greville (*P. conicus*, *P. elegans*, *P. oblongus*, *P. nitidus*, *P. major*, *P. splendidus*), Rattray's taxa (*P. major* var. *densa*, *P. nitidus* var. *armata*, *P. splendidus* var. *marginata*), *P. corniger* Brun, and *P. stolterfothii* Castracane. As Grunow suggested (Grunow in Schmidt 1881, pl. 66, fig. 6), we believe that *Craspedodiscus ovalis* Grunow belongs to *Porodiscus splendidus* Greville. The specimen illustrated by Grunow is slightly oval and has a well defined depressed central area bordered by a rim. All these species are the focus of this paper.

We agree with Mann (1907:237) that *P. calyciflos*, *P. interruptus*, and *P. hirsutus* do not belong



in *Porodiscus*. We also doubt that *Porodiscus minor* and *Porodiscus venkataraminii* Prema and Desikachary (1989) belong to *Porodiscus*, as these species are only slightly depressed at the center with the central area that is not surrounded by a hyaline rim. As argued by Mann (1907), *Porodiscus coronarius* (Mann) Mills 1934 (based on *Melosira coronaria* Mann) does not belong in *Porodiscus*. Specimens identified by Jousé (1954:128, pl. 3, fig. 1–2) as *Porodiscus pliocenicus* (an invalid name) do not belong in *Porodiscus* and were later placed in the genus *Cosmiodiscus* by Jousé (1961).

### MATERIALS AND METHODS

The following slides were examined:

#### British Museum slides

- BM 10602. Coll. Deby. L.H. no. 714. Barbados, Diatomaceae selected. *Porodiscus splendidus*.  
 BM 10603. Coll. Deby. Named by Greville no. 10. "L.H. no. 715. Barbados Diatomaceae selected. *Asterolampra affinis*."  
 BM 10604. Coll. Deby. Named by Greville no. 19. "L.H. no. 716. Barbados. Diatomaceae selected. *Porodiscus splendidus*."  
 BM 10605. Coll. Deby. Named by Greville no. 17. "L.H. no. 714. Barbados. Diatomaceae selected. *Porodiscus splendidus*."  
 BM 10399. Coll. Deby. "L.H. no. 505. Springfield Estate, Barbados. Diatomaceae selected. *Porodiscus splendidus*."  
 BM 2045. Coll. Greville. "Barbados Earth. *Porodiscus ovalis*."  
 BM 2745. Coll. Greville. "Bridgewater. Barbados. Johnson. *Porodiscus conicus*."  
 BM 2744. Coll. Greville. "Cambridge. Barbados. Johnson. 1863. *Porodiscus nitidus*."  
 BM 2751. Coll. Greville. "Bridgewater. Barbados. Johnson. *Porodiscus nitidus* — Holotype."  
 BM 2812. Coll. Greville. "Cambridge. Barbados. Johnson. 1862. *Porodiscus conicus*."  
 BM 2844. Coll. Greville. "Cambridge. Barbados. Johnson. 1863. *Porodiscus major* — type."

#### CAS Collection, Barbados

- CAS 611174. Joe's River. St. John District. 13°13'N, 59°32'W.  
 CAS 611205, CAS 611235. Cambridge Estate, Adams Hill, St. James District.  
 CAS 611193, Springfield. St. Peter District.  
 CAS 611223, CAS 611226. Chimborazo village.

#### Collection N. Strelnikova

- Sample CAS 624819, DSDP Leg 21, 206–16–5, 111–113 cm, Tasman Sea (Middle Eocene).

#### Collection A.P. Olstinskaya

- Sample 74163, Ukraine, Settlement Staroverovka, Kievskaya Formation, middle-upper Eocene.

#### Coll. L.H. Robinson (slides)

- At CAS, received from the New York Botanical Garden.

### NOTES ON COLLECTIONS

The history of collections from Barbados of the British Museum and the Diatom Collection of CAS is very interesting and is described by J.H. Robinson (1934, 1936, 1941). She indicates the absence of good information about the exact locality and the geological position of the samples that Dr. Davy collected in 1846 and sent to R.K. Greville under the name "Barbadoes Earth": "more than two hundred and fifty of these are from Barbados fossil deposit and more than two-thirds of these are cited as "Cambridge Estate" in slides communicated by C. Johnson Esq. From one sample of earth received by Mr. Johnson, the majority of the new species were obtained. Although it was never definitely ascertained where this good sample came from, Dr. Greville seems to have

been under the impression that it was picked up on the Cambridge Estate" (Robinson 1934:3).

The samples from Barbados at CAS were received from J.H. Robinson. She provided information about the localities Joe's River Estate (Robinson 1941, V, p. 1), Springfield (Robinson, 1941, VI, p. 84), and Cambridge Estate (Robinson 1941, VII, p. 181) and gave a list of the species she observed in these localities.

#### MICROSCOPY

Specimens were photographed and examined under light microscopy (Leica DMRB) and by scanning electron microscopy (SEM) (Leo 1450VP).

#### SYSTEMATIC ACCOUNT

***Porodiscus splendidus* Greville, 1865: 46, pl. V, fig. 5.**

(Figs. 1–7, 9–10, 24–33)

Synonyms (taxonomic):

*Craspedodiscus ovalis* Grunow in Schmidt, 1881, Atlas Diat., Taf. 66, fig. 6.

*Porodiscus splendidus* var. *marginatus* Ratray, 1890:672.

This species was described by R.K. Greville from the Springfield Estate, Barbados. Picked valves of this species are arranged among the selected valves of different species on the type slide from the British Museum. Williams (1988:45) indicates that the lectotype is on slide BM 10602 (L.H. no. 714). Greville wrote on the slide the words "Diatomaceae selected. *Porodiscus splendidus*." This species was also selected and marked by Greville on slides: BM 10604 (L.H. no 716, named by Greville no. 19) and BM 10605 (L.H. no. 717, named by Greville no. 17). All slides mentioned above are from Deby's collection and have no locality information. Slide BM 10399 (L.H. no. 505), however, also from Deby's collection bears the notes: "Springfield Estate. Barbadoes. Diatomaceae selected. *Porodiscus splendidus*."

**OCCURRENCE.**— In the material from Barbados at CAS, *Porodiscus splendidus* was found at all localities in Barbados (Springfield, Joe's River, Cambridge and Chimborazo) but more often in the Joe's River material. *Porodiscus splendidus* is the *Porodiscus* species that is the most often cited in contemporary literature (Glezer et al. 1965; Glezer 1969, 1974; Glezer and Jousé 1974; Olshtynskaya 1976; Jousé et al. 1977; Gombos 1983; Fenner 1985; Strelnikova 1992). The distribution of *P. splendidus* (based on the literature) indicates that it is confined to middle Eocene sediments. However, the accuracy of this distribution is in question as the species occurrence may be poorly documented and identification inaccurate.

Our SEM and light microscope (LM) observations add more detail on the valve morphology of this species.

**DESCRIPTION.**— We measured all the valves (a total of 6 specimens) of *Porodiscus splendidus* in Greville's slides (BM 10602, BM 10399, BM 10604, BM 10605, BM 2844), and a total of 50 valves from Barbados sediments in the CAS collection, mostly from Joes's river (CAS 611174 [1345], slides 581128–581131), but also from Springfield (CAS 611193 [3368], slide 581122), Cambridge (CAS 611205 [3142, 3143, 3144], slides 581107, 581108, 581109; CAS 611235 [3375, 3376], slides 581111–581113) and Chimborazo (CAS 611226 [3088, 3089, 3090], slides 581116–58118; CAS 611223 [3570], slide 581101).

The valves are convex, sometimes almost hemispherical, round or slightly oval 30–91  $\mu\text{m}$  in diameter. A deeply concave cavity (4–18  $\mu\text{m}$  in diameter), which is sometimes a little eccentric in outline, is positioned in the center of the valve. The central concave part or "apparent orifice" (or 'sack') juts into the frustule to different depths (6–16  $\mu\text{m}$ ). The ratio diameter of valve/diameter of

center ranges between 3 and 12. There is no apparent correlation between the diameter of the center and the depth of the “sack.” Usually, the center is surrounded by a hyaline ring crest, but this ring is sometimes absent (Fig. 26). Areolae are arranged in radial rows 4–5 (sometimes 6) in 10  $\mu\text{m}$ . Rattray (1890:672) noted that areolae are a little larger at semi-radius, however, this is not confirmed by our observations. Areolae loculate, locula pear-shaped, diameter of foramen about 1  $\mu\text{m}$ . Velum not observed. Rimoportulae arranged on the margin of the valve at distances of 1 to 3–4 areolae from the margin (Figs. 28–29), with 3–4 areolae between rimoportulae. Rimoportulae open externally as small round holes (Fig. 26). Internally, they appear as simple small round holes, but it is not clear from our observations whether they are broken. Valves have no spines, only some protuberances around the areolae (Figs. 24–25). Girdle band is high (12–18  $\mu\text{m}$ ) with a group of vertical lines separated by narrow hyaline lines, 14–18 pores in 10  $\mu\text{m}$  in a line (Figs. 31–33). These observations are consistent with Greville’s original description, and Rattray’s subsequent description (Rattray 1890:672).

**COMMENTS.**—*Craspedodiscus ovalis* Grunow (= *Porodiscus splendidus* var.?) (Schmidt, 1881, Atlas Diat., Taf. 66, Fig. 6) from Springfield is a slightly oval specimen identical in shape and structure with *P. splendidus* Greville. Rattray (1890:672) treated *Craspedodiscus ovalis* Grunow as a variety of *Porodiscus splendidus* and named it *Porodiscus splendidus* var. *marginata*. Based on our observations of round and slightly oval valves of *P. splendidus* in BM and CAS materials, and Greville’s original description of *P. splendidus* (“disc circular, occasionally broadly oval”) we treat here *Craspedodiscus ovalis* Grunow (= *Porodiscus splendidus* var. *marginata* Rattray) as a synonym of *Porodiscus splendidus* Greville.

***Porodiscus splendidus* var. *corniger* (Brun) Fournanier, new comb.**

(Figs. 37–40)

Basionym: *Porodiscus corniger* Brun, 1896:242, pl. XIX, fig. 15.

*Porodiscus corniger* Brun (1896:242, pl. XIX, fig. 15) (Figs. 37–40) was described from Chimborazo, Mount Hillaby, as a very rare form. Brun noted its similarity with *P. splendidus*, the two taxa differing only by the presence of spines in *P. corniger*. The valves of *Porodiscus* in the Chimborazo material are very rare. Only one frustule of *P. corniger* was observed in the Chimborazo material (CAS 611226); it was mixed with several forms without spines. As the two types are identical in structure and dimensions and differ only by the presence of spines, we believe that *P. corniger* should be treated as a variety of *P. splendidus*. Since we did not observe a continuum of morphological expressions between specimens with spines and specimens without spines, we are recognizing *P. splendidus* var. *corniger* and *P. splendidus* var. *splendidus* as two separate taxonomic entities.

***Porodiscus splendidus* var. *excentricus* (Olshtinskaya) Olshtinskaya, new comb.**

(Figs. 8, 11–12, 34–36)

Basionym: *Porodiscus nitidus* var. *excentricus* Olshtinskaya, 2001:452, pl. I, figs. 1–3.

Olshtinskaya (2001) described a new diatom taxon from the upper Eocene sediments of the Pristen village, Ukraine, as a variety of *Porodiscus nitidus* (*Porodiscus nitidus* var. *excentricus*).

We studied specimens from Staroverovka (coll. A.P. Olshtinskaya) near the type locality of her taxon and in the same geological interval (Kievskaya Formation, middle to upper Eocene). Olshtinskaya’s taxon differs from *Porodiscus splendidus* only by the eccentric position of the “sack.” In the material from Barbados, there are a few forms with an eccentric “sack.” In the



Ukrainian material, however, the eccentric type is dominant, and the external surface of Ukrainian forms are smooth, without small bumps.

***Porodiscus nitidus* Greville, 1863, p. 65, pl. IV, fig. 4.**

(Figs. 13–16, 41–56)

Synonyms:

*Porodiscus nitidus* var. *armatus* Rattray, 1890:672–673, pl. III, fig. 17.

*Porodiscus spiniferus* Rattray, 1890:674, pl. III, fig. 19.

Greville described *P. nitidus* from the Cambridge Estate. Two slides in the Greville collection (slides BM 2751 and BM 2744) bear the indication “*Porodiscus nitidus*.” Slide BM 2751 is a smear slide and, according to Williams (1988), is the probable holotype slide for *P. nitidus*. The slide bears no locality information besides “Barbadoes. Johnson Coll. Greville.” *P. nitidus* is also present in slide BM 2812.

Greville (1863:65) stated in his original description of *P. nitidus*, “Disc convex, unarmed, the longest lines of puncta single (not in pairs), alternating with two or three series of shorter ones; puncta distinct, all of them becoming much more minute towards the margin. Diameter .0026. Barbadoes deposit, from Cambridge Estate; C. Johnson Esq. . . . It is a scarce species.”

*Porodiscus nitidus* var. *armatus* Rattray (1890:672–673) was also described from the Cambridge Estate. Rattray noted the presence of spines (“spines acicular, about .01 mm., long, sometimes shorter, inserted about  $\frac{3}{4}$  of radius from center”). It appears from Rattray’s description and illustration that the main difference between *P. nitidus* var. *armatus* and the nominal variety is the presence of spines. The two varieties are otherwise identical in valve structure and dimensions. *Porodiscus spiniferus* Rattray (1890:674) was also described from the Cambridge deposit. It appears from Rattray’s description that *P. spiniferus* is similar to *P. nitidus* var. *armatus*, but it has more robust spines, more evident fascicles, and possibly more dome-shaped valves.

Although Greville 1863 was clear in his original description of *Porodiscus nitidus* that spines were not present (“unarmed”), the slides in his collection (BM 2751, BM 2744) feature both specimens with spines and without spines. Our observations indicate that there is a continuum between specimens lacking spines, specimens with minute spines, and specimens with robust spines. There is also a great variability in the appearance of the fascicles, from very faint to evident. Despite three taxa having been described for this material, our observations suggest a continuum of morphological expressions within a single taxon, and support the synonymy between *Porodiscus nitidus* var. *nitidus*, *P. nitidus* var. *armatus* and *P. spiniferus*.

Our description of *P. nitidus* is supported by the observation of 12 specimens (on 11 slides) from Barbados from slides at the British Museum (BM 2744, BM 2751, BM 2745, BM 2812) and at CAS (CAS 61174[1345], Joe’s River, slide 581129; CAS 611235[3376], Cambridge, slide 581112; CAS 611226[3089], Chimborazo, slide 581117). We found the best preserved specimens of *P. nitidus* in DSDP Leg 21, Sample 206-16-5, 111–113 cm, Tasman Sea (CAS 624819), from which we studied 25 valves in LM and SEM.

**DESCRIPTION.**— Valves circular, convex, 40–118  $\mu$ m in diameter, with a deeply concave central part, round or very slightly oval, 5–7  $\mu$ m in diameter that is either surrounded by a hyaline ring or lacks a ring. Ratio valve diameter/diameter of center 8–20. Areolae loculate with external cribrum and internal foramen, 5–8 in 10  $\mu$ m. Loculae cylindrical. Areolae arranged in radial rows, 5–8 in 10  $\mu$ m in a row, organized in fascicles, separated by hyaline lines. Fascicles are usually faint, sometimes more distinct. The hyaline lines and fascicles may be more distinct internally. Valve surface smooth or with spines. There is great variability in the size of the spines from barely notice-

able to very long. Spines are situated on the hyaline lines at mid-radius or closer to the margin ( $\frac{3}{4}$  of radius from center according to Rattray's original description) (Figs. 41–42). Rimoportulae are positioned in the hyaline lines at the distance of 1 areola from the valve margin (Fig. 56). They consist of small round holes externally, and small round or oval holes internally. It is possible, however, that they are eroded. Cribrum consists of several pores. In well preserved cribra there are 5–7 marginal pores surrounding a single (but sometimes 2–3) central pore (Figs. 52–55). Rattray (1890:672) noted that the areolae were more dense near the margin; however, this is not confirmed by our observations.

**COMMENTS.**— Sims (1989:366, figs. 48–52) published SEM photos on specimens identified as *P. nitidus* var. *armatus* Rattray from Joe's River, Barbados (material from CAS collection: A.L. Brigger's samples, presented to British Museum by R.W. Holmes). Her specimens have spines, but unlike the specimens we observed, there are several spines on one hyaline ray. Spines nearest to the center (ca  $\frac{1}{4}$  radius) are long and thick, spines closer to the margin are of moderate size. The presence of more than one concentric row of spines in *P. nitidus* was not observed by us and not mentioned by Rattray in the description of *P. nitidus* var. *armatus* or *P. spiniferus*. This suggests that the specimens illustrated by Sims may belong to a different taxon. Further study of her population is needed to determine if it represents a separate taxonomic entity.

The main differences between *P. nitidus* and *P. splendidus* are:

1) The ratio of valve diameter to diameter of the concave center, which is smaller for *P. splendidus* (3–9) and larger for *P. nitidus* (9–18). The diameter of the center is therefore larger in *P. splendidus* (5–18  $\mu\text{m}$ ) than in *P. nitidus* (4–6  $\mu\text{m}$ );

2) Areolae are larger in *P. splendidus* (4–6, commonly 5 in 10  $\mu\text{m}$ ) than in *P. nitidus* (5–8, commonly 6–8 in 10  $\mu\text{m}$ );

3) Areolae are arranged in radial lines in both species, but *P. nitidus* has slightly more evident fasciculae, which are separated by hyaline lines that are more distinct internally;

4) Spines are absent in *P. splendidus*, they are often (but not always) present in *P. nitidus*.

***Porodiscus conicus* Greville, 1863: 65, pl. IV, fig. 3.**

(Figs 17, 18, 64?)

Synonym:

*Porodiscus elegans* Greville, 1863:64, pl. IV, fig. 1.

This species was described by Greville from Cambridge Estate, Barbados. We studied it only from the type slides of the British Museum as we did not find any specimen in the CAS Collection material from Cambridge, Barbados. This species has not been reported since Greville's work. A complete frustule is present in slide BM 2812, the holotype according to Williams (1988). We also found this species on slides BM 2744 and BM 2745. We did not find definite specimens of this species in the CAS Collection.

**DESCRIPTION.**— Greville's description is short: "Small; disc conical, unarmed, with an obtusely truncate apex; radiating lines of puncta extremely minute. Diameter .0014" [36  $\mu\text{m}$ ]." In the comments to this description Greville writes — "The smallest of the species hitherto discovered, and occurring not infrequently in perfect frustules. The length of the connecting zone is considerable, and that of the entire frustule, when both valves are symmetrical, about .0040" [98  $\mu\text{m}$ ]. The valve is decidedly conical, but obtusely truncate at the top when seen in profile. It hardly ever happens that the valves are equal in the same specimen. Indeed, I do not think that I have seen a single example perfectly symmetrical, one valve being almost always considerably shorter than the other. The length of the connecting zone gives the frustule a cylindrical appearance."

The diameter of the specimen illustrated by Greville is 45  $\mu\text{m}$ . Rattray (1890) restudied Greville's and Johnson's material and added to Greville's description: "Diameter .025 to .0525 mm. Major axis of frustule from .0625 to .0875 mm. Surface a more or less elongate regular cone, transversely truncate at the extremities, the opposite valves of a frustule of unequal height. Central space? Markings obtusely angular or subareolate, 6 in .01 mm, subequal; rows radial, straight, non-fasciculate; secondary oblique decussating rows evident, from the truncated ends of the cone a few short tapering clear lines, distinct. Girdle cylindrical, from .025 to .0325 mm, broad; a narrow band at each extremity, hyaline, the intervening portion clouded with diffuse parallel lines."

In Greville's slides, we found the valve diameter of *Porodiscus conicus* to range between 40–43  $\mu\text{m}$ , the height of conical valves to be 30–35  $\mu\text{m}$ , the height of the second valve to be 16  $\mu\text{m}$ , and the girdle band to be 27–32  $\mu\text{m}$  in width. Areolae on the valves are arranged in radial rows, 7–8 in 10  $\mu\text{m}$  in a row, 8 rows in 10  $\mu\text{m}$ . On the shorter valve 5–6 rows of areolae alternate with thin hyaline lines.

**COMMENTS.**—Greville (1863:64) described *Porodiscus elegans* from Cambridge and other localities. "Disc very convex, unarmed, divided into compartments by pairs of the radiating lines of very minute puncta, extending from the margin to the centre. Diameter .0020" [51  $\mu\text{m}$ ] to .0033" [84  $\mu\text{m}$ ]." The specimen illustrated by Greville has a diameter of 77  $\mu\text{m}$ . Greville (1863:64) commented: "This species is distinguished by the disc being divided into numerous compartments, by pairs of radiating lines of puncta, very distinctly seen under a moderately magnifying power, and at the same time being quite destitute of spines. It is the most frequent species, three or four valves sometimes occurring in a single slide. The connecting zone is rarely seen *in situ*." Rattray (1890:673) added: "Circular. Diameter .0625 to .095 mm. Surface rounded and dome-shaped. Central space circular, .0075 mm. broad, sharply defined, hyaline. Markings obtusely angular or subareolate, decreasing gradually from the central space outwards, around the central space 6, near the border 10 to 12, in .01 mm; rows radial, straight; fasciculi distinct; interspaces minute, largest around the central space. Girdle cylindrical, .03 mm, broad, in a frustule, .06 mm in diameter; a narrow hyaline band at each extremity; the interval minutely punctate; at subregular intervals narrow hyaline straight lines at right angles to the edges of the valve. The fasciculi are bounded by two adjacent radial rows, somewhat more conspicuous than the intervening rows. In one of the valves in Greville's collection it is possible to trace downwards from the central space a cylindrical siliceous tube which is of sufficient length to have passed to a plane corresponding in position to the edges of the valve." Our measurements of the specimen from slide BM 2745, the holotype of *Porodiscus elegans* according to Williams (1988) are: diameter of valve 45  $\mu\text{m}$ , diameter of center 8  $\mu\text{m}$ , areolae in a row 7 in 10  $\mu\text{m}$ .

*Porodiscus conicus* and *P. elegans* are found on the same slides (BM 2812 and BM 2745). The non-conical valve of *P. conicus* seems identical to valves attributed to *P. elegans*. They both have a fasciculate arrangement of areolae and the same areolae density. Given that the two morphologies occur together as part of a single frustule, we believe that *P. conicus* and *P. elegans* are conspecific. We treat the two names as synonyms and retain *P. conicus* for the name of the species, since it was originally applied to a complete frustule.

***Porodiscus major* Greville, 1863: 64, pl. 4, fig. 2.**

*Porodiscus major* was described from Cambridge Estate, Barbados, from a slide communicated by C. Johnson (Greville 1863:64). The description was later amended by Greville (1865:46–47). We did not study this species as we did not find any additional specimens besides the valve on slide BM 2844 (holotype?) that was illustrated by Williams (1988, pl. 52, figs 5–6). Based on our observations of slide BM 2844, we believe that this species belongs in *Porodiscus*.



***Porodiscus oblongus* Greville, 1863: 65, pl. 4, fig. 5.**

(Figs. 22–23, 57–61)

Nomenclatural synonyms:

*Porodiscus ovalis* Greville, 1863, explan. pl. 4, fig. 5 (alternate name).*Craspedodiscus oblongus* (Greville) Grunow in Schmidt, 1881, explan. pl. 66, Figs. 7–9.

Greville (1863:65) described *Porodiscus oblongus* from “Barbadoes deposit” and illustrated it as *P. ovalis* (Greville 1863, explan. pl. 4, fig. 5). Slide BM 2045 bears the note “Coll. Greville. Barbadoes earth” and the name “*Porodiscus ovalis*.” Williams (1986) cites this slide as possibly the holotype. This species is not rare in the British Museum slides. On slides BM 10602 and BM 10399, valves of *P. oblongus* were selected (picked) by Greville.

Greville’s original description is short (Greville 1863:65): “Disc elliptical-oblong; pseudo-opening large. Long diameter about .0028” [71  $\mu\text{m}$ ]. He also added, “The pseudo-opening is very large, the radiating lines of granules are less crowded, and the granules themselves larger than in any of the preceding species”. Greville (1865:46) adds to the description: “The diameter of the disc is .0030” [77  $\mu\text{m}$ ]. Radiating cellules about 8 in .001.” The specimen figured in Greville’s original illustration (Greville 1863, fig. 5), has a diameter of 70–35  $\mu\text{m}$ , and there are about 5 areolae in 10  $\mu\text{m}$  on a row. Ratray (1890:674) added to this description: “Subacutely elliptical. Major axis .05 mm long, about 2.5 times minor. Surface sloping gradually downwards from edge of central space. Central space roundly elliptical, with major axis corresponding in direction to minor axis of valve. Markings angular, decreasing regularly and somewhat rapidly from central space to border; around the central space 4.5 at border 10 in .01 mm; rows radial, substraight. Border narrow, hyaline.”

**DESCRIPTION.**— We measured five valves of *P. oblongus* from slides BM 2045, BM 1062, BM 1063, BM 10399, and five valves from sample CAS 611193[3368], Springfield (slide 581122).

Valves oval, length (54–78  $\mu\text{m}$ ) two times larger than width (26–37  $\mu\text{m}$ ), with round or slightly elliptical center (9–11  $\mu\text{m}$  diameter). Areolae organized in rows radiating from the center, 5–6 areolae in 10  $\mu\text{m}$ . Locula with velum better preserved on the elongated ends of the valves (Fig. 58), foramen about 1  $\mu\text{m}$  in diameter (Fig. 60). Velum consisting of a central cribral pore surrounded by 4–6 marginal cribral pores (Figs. 57–58). The central depression (“sack”) is not bordered by a real hyaline ring, but the areolae walls surrounding the depression form a little boundary around it that appears like a ring. Areolae in the depression are smaller than on the valve. Rimoportulae arranged along the margin of the valve, with more distance from the margin in the middle of valve (2–3 areolae from margin) and closer to the margin (1 areola from margin) at the ends of the valve. Rimoportulae opening externally as round small holes, internally also as holes, but may be broken (Fig. 60).

**COMMENTS.**— Castracane (1886) described a similar species *P. stouterfothii* from the equatorial part of the Pacific Ocean as a living species; it differs from *P. oblongus* by a more rhombic shape. Also similar to *P. oblongus* is *Coscinodiscus oblongus* Greville (1866a:4, figs. 9–10) from Springfield Estate, Barbados. Both species (*P. oblongus* and *C. oblongus*) are present in British Museum slides BM 2045, BM 10605, BM 10604, BM 10603, BM 20602 and BM 10399. The main difference between the two taxa is a deeper (steeper) cavity in *Porodiscus oblongus*. *Porodiscus oblongus* Greville from Springfield is illustrated in Schmidt’s Atlas (Schmidt 1881, Taf. 66, figs. 7–9) as *Craspedodiscus oblongus* (Grev.) Grunow [in Schmidt] (a valid new combination). Schmidt also illustrates from Springfield *Coscinodiscus oblongus* Greville (Taf. 66, figs. 10–11) for which he suggests a generic placement in *Craspedodiscus* (“unbedingt zu *Craspedodiscus* zu rechnen”). Schmidt, however, did not validly publish the new combination, which seems to have been first published by Hanna (1931:194).

*Craspedodiscus oblongus* (Greville) Hanna (= *Coscinodiscus oblongus* Greville) and *Craspedodiscus oblongus* (Greville) Grunow in Schmidt (= *Porodiscus oblongus* Greville) are similar species; however, *Craspedodiscus oblongus* (Greville) Grunow in Schmidt belongs to *Porodiscus*, whereas *Craspedodiscus oblongus* (Greville) Hanna belongs to *Craspedodiscus* and had been renamed *Craspedodiscus ellipticus* by Gombos (1982). Fenner (1985) refers to two species, *Craspedodiscus ellipticus* Gombos (= *Coscinodiscus oblongus* Greville) and *Craspedodiscus oblongus* (Greville) Grunow (= *Porodiscus oblongus* Greville). Many works (e.g., Barron et al. 1984; Strelnikova 1992) cite *Craspedodiscus oblongus* (Grev.) Grunow from Middle Eocene sediments, which corresponds to *Coscinodiscus oblongus* Greville (= *Craspedodiscus ellipticus* Gombos). This species has a wide distribution in the Middle Eocene in tropical and non-tropical regions. *Porodiscus oblongus* Grev. has a narrower distribution limited to the tropical region. We found it only in samples from Barbados.

***Craspedodiscus ellipticus* Gombos, 1982, p. 231, figs 13, 14.**

(Figs. 19, 21, 62, 63)

Nomenclatural synonyms:

*Coscinodiscus oblongus* Greville, 1866a:4, pl. 1, figs 9, 10.

*Craspedodiscus oblongus* (Greville) Hanna, 1931:194 (illegitimate name, later homonym).

*Craspedodiscus oblongus* (Greville) Grunow in Schmidt, 1881, caption Taf. 66, figs. 10–11 (invalid name).

Greville's original description is short "Disc more or less oblong, having the center depressed, and an umbilicus containing a number of subremote granules; surface filled up with radiating granules, which diminish in size next the umbilicus and towards the margin, where they resemble minute puncta. Length .0028" to .0050" [71 to 127  $\mu\text{m}$ ]." It was described from Springfield.

**DESCRIPTION.**— We measured several valves from slide BM 10603 and slide CAS 581122 (CAS 611193[3368]).

We found that the valves, characterized by their elongated shape, are 56–67  $\mu\text{m}$  in length, nearly 30  $\mu\text{m}$  in width, with areolae arranged in rows radiating from a concave center, 6 areolae in 10  $\mu\text{m}$  on a row. The concave center is oval, with diameter 10–12  $\times$  6–8  $\mu\text{m}$ . Rimoportulae arranged along the margin, opening externally as a small round holes, and internally also as round holes (they may be broken, however).

**COMMENTS.**— Williams (1988, pl. 28, figs 1–4) illustrated two specimens that he referred to *Coscinodiscus oblongus* Greville. Only the specimen illustrated in figures 3–4 belongs to *Craspedodiscus ellipticus* Gombos (= *Coscinodiscus oblongus* Greville). The other specimen (figs. 1–2), which has a round center, belongs to *Porodiscus oblongus* Greville.

***Craspedodiscus umbonatus* Greville, 1866b:79, pl. 8, fig. 15.**

(Figs. 65–70, 74)

*Craspedodiscus umbonatus* Greville was described from "Cambridge Estate Barbados deposits in slides communicated by C. Johnson Esq." The original description is short: "Disc hexagonally cellulate, the border nearly equal to half the radius, the centre rather sharply umbonate." Greville further commented: "Distinguished at once by its umbonate centre. Cellules near the margin of the border 8 in .001". Williams (1988, pl. 33, fig. 7) illustrated the holotype from slide BM 5469.

**DESCRIPTION.**— We did not study the holotype slide, but this species was common on slides from the CAS Collection, especially from material from Joe's River (CAS 611174[1345], slides 581129, 581130).

The valves are circular, diameter 42–74  $\mu\text{m}$ , convex, sometimes hemispherical with deeply concave center, 7–10  $\mu\text{m}$  diameter. The ration of the valve diameter to the diameter of the center is 6–8. Areolae are arranged in radial rows, 4–5 in 10  $\mu\text{m}$ . External cribrum consists of one or several central pores surrounded by marginal pores. Areolae are a little smaller on the concave center. Rimoportulae are arranged around the margin, opening externally as small round holes, sometimes one of them situated in smaller cavities (Fig. 74) on the margin. They open internally as simple round holes; however, they may be broken. Valves have no spines.

**COMMENTS.**— This species has been reported only from Barbados. *Craspedodiscus umbonatus* differs from *Porodiscus* only by the absence the hyaline ring around the cavities and the little depression for one rimoportula at the margin (Fig. 74).

#### TYPIFICATION OF THE GENUS *PORODISCUS* WITH *PORODISCUS NITIDUS* GREV.

In the original publication of *Porodiscus*, Greville included five species (*P. nitidus*, *P. elegans*, *P. major*, *P. conicus*, and *P. oblongus* = *P. ovalis* in the plate caption), but he did not designate a type. The most common species of *Porodiscus*, *P. splendidus* Grev. is not a candidate as generitype inasmuch as it was not one of the original species. We designate here *Porodiscus nitidus* Grev. as the lectotype of genus *Porodiscus* Greville. Although not as common as *P. splendidus*, *P. nitidus* has been reported in various fossil localities, and it is a better choice than any of the other four species that have never been observed other than on Greville's original slides. The holotype of *P. nitidus* is on slide BM 2751 (Bridgewater, Barbados).

#### DISCUSSION

*Coscinodiscus* Ehrenberg, *Craspedodiscus* Ehrenberg, *Porodiscus* Greville, and *Annellus* Tempère are closely allied genera in the family Coscinodiscaceae; they differ only by the structure and shape of the cavity in the valve center. Based on the shapes and arrangements of the rimoportulae, *Craspedodiscus* and *Porodiscus* are similar. Stratigraphically, *Coscinodiscus* is the oldest of these genera (Cretaceous). *Craspedodiscus* apparently separated from *Coscinodiscus* during the early Paleocene. *Porodiscus* separated from *Coscinodiscus* or *Craspedodiscus* only during the Middle Eocene, whereas *Annellus* is restricted to the Miocene. The Cretaceous genus *Pomphodiscus* Barker and Meakin has locular areolae, and a central cavity that is reminiscent of some species of *Porodiscus* and *Craspedodiscus*. The central cavity in *Pomphodiscus* is a chamber that is formed by an inflation and separation of the basal siliceous layer into two layers. The shape and the central position of the rimoportulae, however, places this genus in the family Stellarimaceae (Nikolaev and Harwood 2000). Even more distant in the classification, but with a central chamber, is the Cretaceous genus *Benetorus* (family Stictodiscaceae). The uvular process of the Early Cretaceous genus *Archaeogladiopsis* (family Archaeogladiopsidaceae) is also reminiscent of the cavity of *Porodiscus*. The uvular process, centrally located is a funnel-shaped depression with a round opening in the valve exterior and a uvula-shaped intrusion on the inside, without visible openings (Nikolaev and Harwood 1997). We believe that the higher level classification of these fossil genera is still valid (i.e., we are not suggesting that these genera are closely related), and that their superficial similarities are due to parallel evolution.

The following section will concentrate on the morphological differences between *Porodiscus* and *Craspedodiscus* and between *Annellus* and *Craspedodiscus*, because it is presently difficult to separate them.



### *Craspedodiscus* Ehrenberg

We recognize three informal divisions among the diatoms that have been referred to *Craspedodiscus*. The classical concept of *Craspedodiscus* is represented by *C. coscinodiscus* (Figs. 81–86) and is characterized by a large internal depression that has a diameter that is at least one half of the entire valve. The central depression typically has a nearly flat bottom and has areolae that are reduced in size compared to those of the outer valve surface (Figs. 84–85). The transition from the outer valve surface to this internal depression is abrupt, often close to 90° (Figs. 82–85). Similar to *Porodiscus*, a hyaline rim occurs at this transition (Figs. 82–85) in most Miocene forms. The edge of the central depression is rough, as if a weakly silicified covering, now missing, was present over a chamber in that species. Such covering was never observed in *Craspedodiscus*.

The majority of diatoms that have been referred to *Craspedodiscus* comprise a second group, represented by *C. elegans*, the lectotype of *Craspedodiscus* (see Ross in Farr et al. 1979). Diatoms of this group have an internal depression that is less distinct, characterized by a more gradual transition from the valve's mantle and by areolae that are not distinctly different from those on the valve's margin. Some Oligocene diatoms that have traditionally been referred to *Craspedodiscus coscinodiscus*, but are better assigned to *Craspedodiscus barronii* Bukry (Figs. 76–77), have gently sloping central depressions and could be referred to this group. Other taxa, including *Craspedodiscus undulatus* Gombos, *C. elegans* Ehrenberg and *C. moelleri* A. Schmidt, have undulated valve surfaces, reminiscent of the undulated valve surfaces of certain species of *Actinocyclus* and *Cestodiscus*. Diatoms of this group appear to be closely related to *Coscinodiscus*, and it is not clear why they should be separated from it. Indeed, *Coscinodiscus excavatus* (Fig. 92) might be placed in this group, although no formal transfer to *Craspedodiscus* has been proposed. We do not, however, wish to discuss the taxonomic implications of transferring *Craspedodiscus elegans* and other diatoms of this group to *Coscinodiscus* in the present paper.

A third group of taxa that have been referred to *Craspedodiscus* are similar to *Porodiscus* in that they possess a distinct internal depression that is typically confined to only the centermost portion of the valve. This group is represented by *Craspedodiscus ellipticus* Gombos (= *Coscinodiscus oblongus* Greville) (Figs. 62–63) and *C. umbonatus* Greville (Figs. 65–70). As in *Porodiscus*, the central depression is deeply invaginated with a concave central valvar surface. The transition from the outer valve surface to the interior depression, however, is not as abrupt as in *Porodiscus*, and no hyaline ring is present. Valves of *Craspedodiscus ellipticus*, with their sloping central depression (Figs. 62–63), clearly differ from valves of *Porodiscus oblongus* (Figs. 57–61) with their central depression more circular and sloping more abruptly. On his Figure 17, however, Gombos (1982) illustrates a diatom, which he refers to *Craspedodiscus oblongus* (Greville) Schmidt, which has a circular internal depression like that of *P. oblongus*, but it also possesses a gradual or sloping transition from the outer valve surface, as in *C. ellipticus*. This specimen may be transitional between *P. oblongus* and *C. ellipticus*.

### *Annellus* Tempère

The genus *Annellus* is restricted to the late-early and early-middle Miocene, separated by at least 15 million years from the Eocene records of *Porodiscus*. At present, *Annellus* is monospecific, with *A. californicus* Tempère, as the only species. As discussed by Ryde (1962), *Annellus* is closely related to Miocene forms of *Craspedodiscus coscinodiscus*.

Ryde (1962) made a detailed morphologic study of *Annellus californicus* Tempère, noting that the valve was “formed of an outer cylinder inturned at one end (and) deeply invaginated to produce within the first, a co-axial cylinder closed at the lower end.” He mentioned that the “inner cylinder

often tends to bulge somewhat and its length is equal to the depth of the valve mantle," appearing as a dome when viewed from the inside of the valve. Ryde (1962) stated that the diameter of the areolae on the valve surface of the inner cylinder is very much reduced in size compared to those of the valve mantle and the surface consists of rather fragile, diaphanous silica that is often not preserved. Ryde (1962) further commented on the rather abrupt transition from the inner valve mantle to the inner cylinder. Based on comparison with the internal valve surface of *Craspedodiscus coscinodiscus*, Ryde (1962) chose to transfer *Annellus californicus* Tempère to *Craspedodiscus californicus* (Tempère) Ryde. We feel, however, that the high mantle of *Annellus californicus*, which results in valves often being orientated in valve view on slides, is a unique feature to *Annellus*, distinguishing it from the *Craspedodiscus coscinodiscus* group. *Annellus* also lacks the hyaline rim, which is present in typical forms of *Craspedodiscus coscinodiscus* (Figs. 82–86). Barron (1983) argued that the shallower mantle of his new species, *Craspedodiscus rhydei*, warranted placing it into *Craspedodiscus* rather than *Annellus*; however, *C. rhydei* (Fig. 91) clearly lacks a hyaline ring and closely resembles valves of *Annellus californicus* (Figs. 87–88).

### CONCLUDING REMARKS ON *PORODISCUS* GREVILLE

*Porodiscus* resembles both *Coscinodiscus* and *Craspedodiscus* with the presence of locular areolae with external cribrum and internal foramina, and marginal rimoportulae. It has unique characters, however, such as spines (in some species), which are not present in *Coscinodiscus* nor in *Craspedodiscus*. The central cavity, which also characterizes *Craspedodiscus*, seems to be of a different nature in *Porodiscus*, where it is very steep (tube-like) and well defined, being bordered by a hyaline rim. *Craspedodiscus* species usually do not have such hyaline rims (except for some tropical Miocene forms of *Craspedodiscus coscinodiscus*) and lack a well-defined central depression. The hyaline rim in these forms may be the edge of a broken outer surface of a chamber. Miocene forms of *Craspedodiscus coscinodiscus* and *Annellus californicus*, which have a well defined central depression, typically have a central depression that covers at least half of the diameter of the valve. This character, and the separation in geologic time of more than 15 million years between the Eocene forms of *Porodiscus* and the Miocene forms of *Craspedodiscus coscinodiscus* and *Annellus*, are arguments in support of *Porodiscus* being retained as a valid taxonomic entity.

### ACKNOWLEDGMENTS

We thank Dr. David Williams of the British Museum who made possible the study of the type slides of R. Greville. The work was supported by Russian Fund for Fundamental Research (RFFI) Grant 00-04-49333 and the Diatom Collection of the California Academy of Sciences. We are also thankful to D. Ubick, Scott Serata, M. Potapova, and E. Ruck for assistance in the preparation of this article, Dr. David Harwood for his review of the manuscript and helpful suggestions, and Dr. Michele L. Aldrich, who read the near final version of the manuscript and saved us from memorializing a number of grammatical and other baby blunders.

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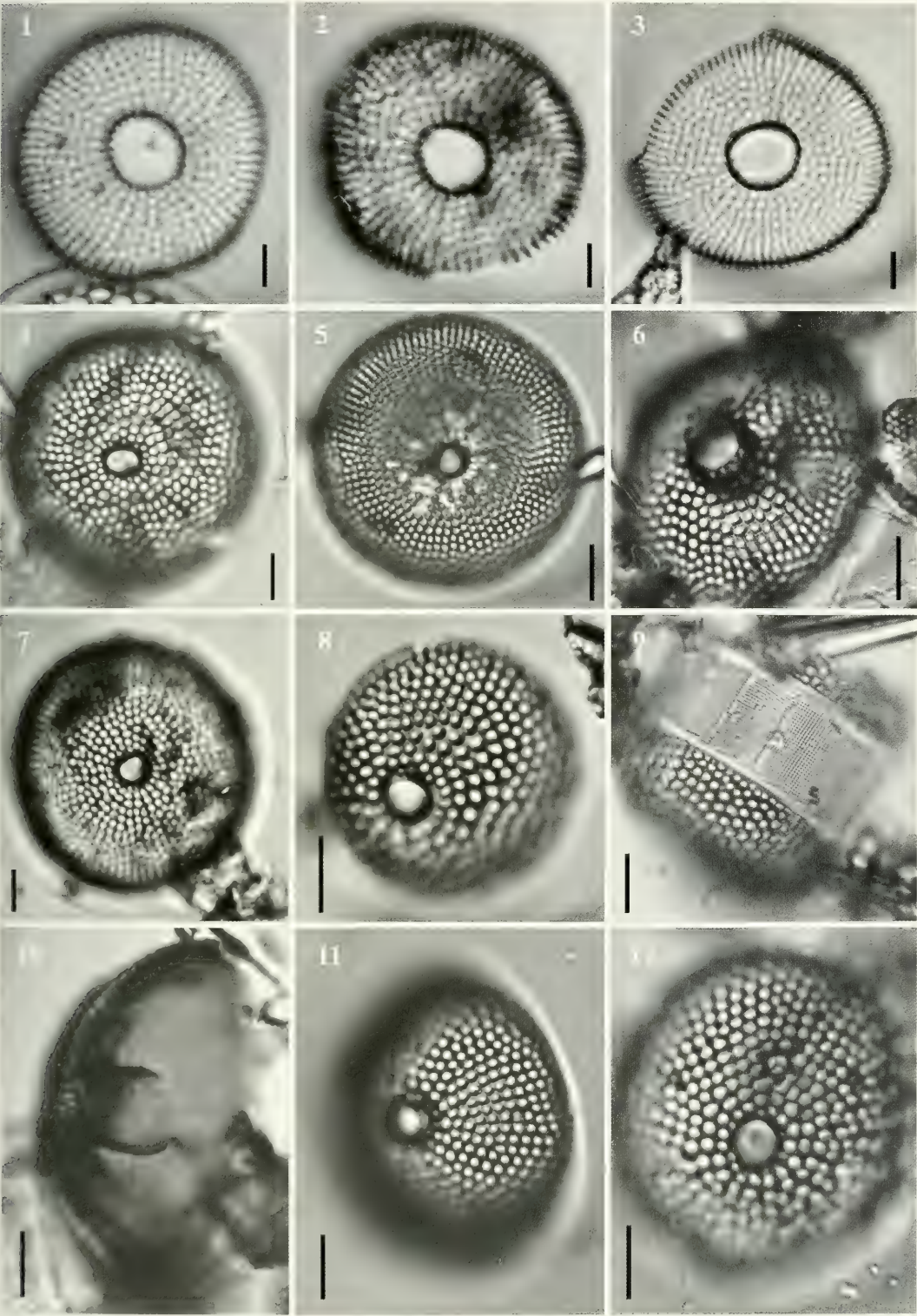
## PLATES

## PLATE 1

Light microscopy. **Figures 1–7, 9–10.** *Porodiscus splendidus* Greville. Figure 1. Lectotype (internal view), BM 10602. Figures 2, 3. BM10399. Figure 4. CAS 611235 (Cambridge). Figure 5. CAS 611174 (Joe's River). Figure 6. CAS 611174 (Joe's River). Figure 7. BM 2844. Figure 9. CAS 611235 (Cambridge). Figure 10. CAS 611193 (Springfield). **Figures 8, 11, 12.** *Porodiscus splendidus* var. *excentricus* (Olsht.) Olshtinskaya new comb. Figure 8. Olst. Collection, Ukraine, Staroverovka. Figure 11. CAS 611174 (Joe's River). Figure 12. CAS 611174 (Joe's River).

Scale bars = 10  $\mu\text{m}$ .



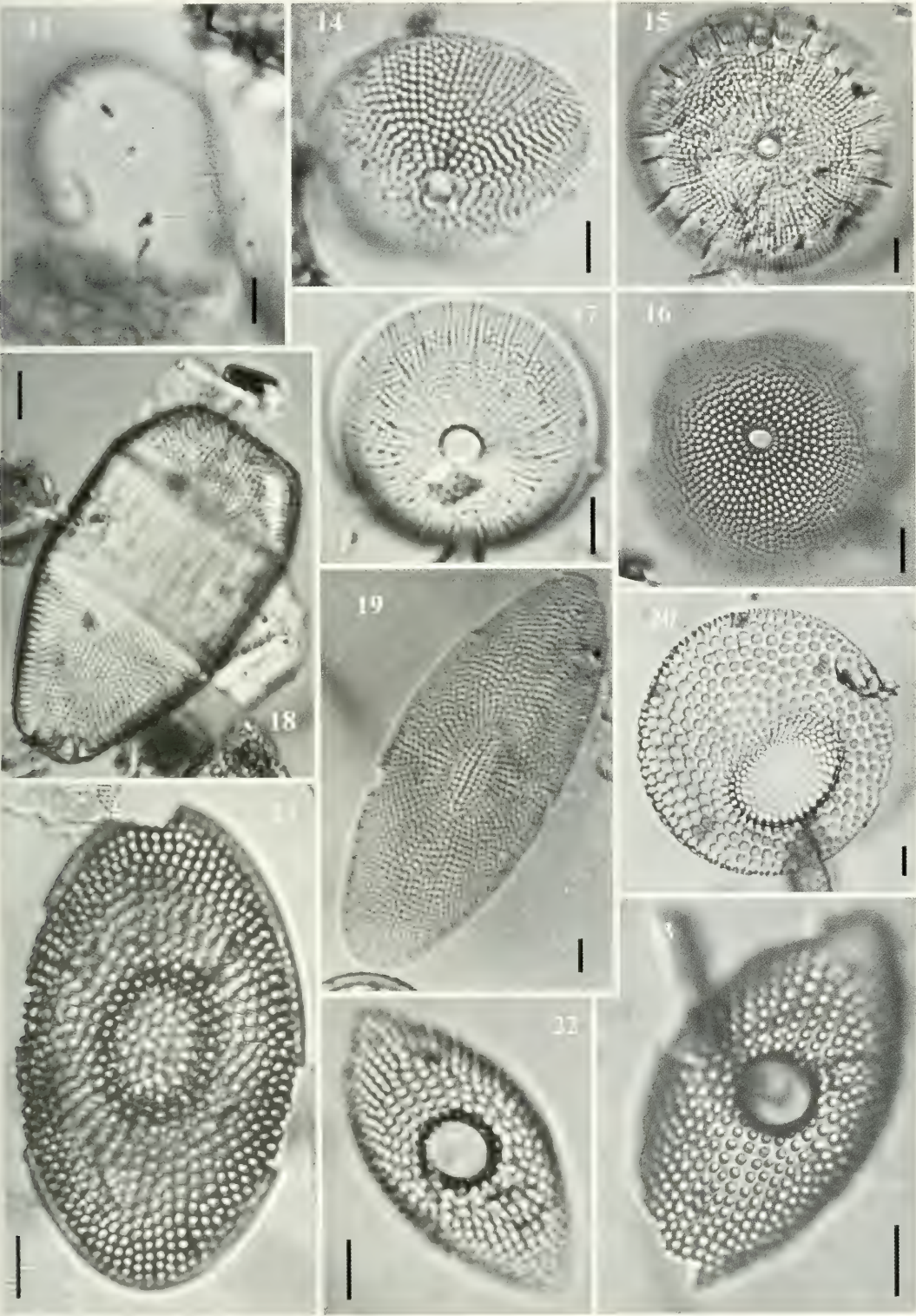


## PLATE 2

Light microscopy. **Figures 13–16. *Porodiscus nitidus* Greville.** Figure 13. Valves with spines. BM 2751. Figure 14. Valves with no spines. BM 2751. Figure 15. Valves with spines. BM 2812. Figure 16. Valves with no spines. CAS 611174 (Joe's River). **Figure 17. *Porodiscus conicus* Greville.** (non-conical valve; Synonym: *Porodiscus elegans* Greville.) BM 2745. **Figure 18. *Porodiscus conicus* Greville.** BM 2812. Holotype. **Figures 19, 21. *Craspedodiscus ellipticus* Gombos.** Figure 19. BM 1063. Figure 21. CAS 611193 (Springfield). **Figure 20. *Coscinodiscus excavatus* Greville.** BM 2745. **Figures 22–23. *Porodiscus oblongus* Greville.** Figure 22. BM 2045. holotype? Fig 23. CAS 611193 (Springfield).

Scale bars = 10  $\mu$ m.



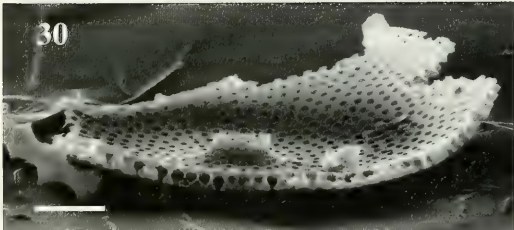
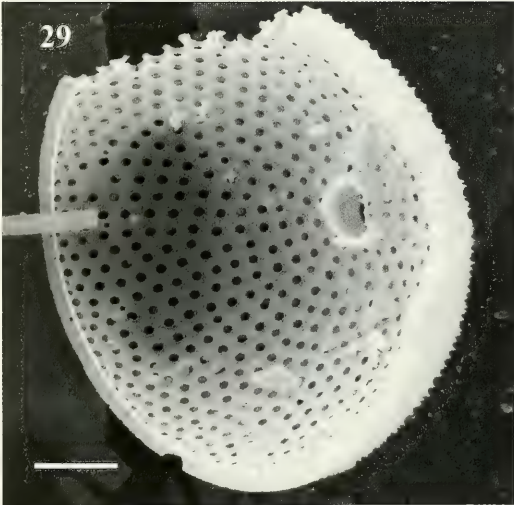
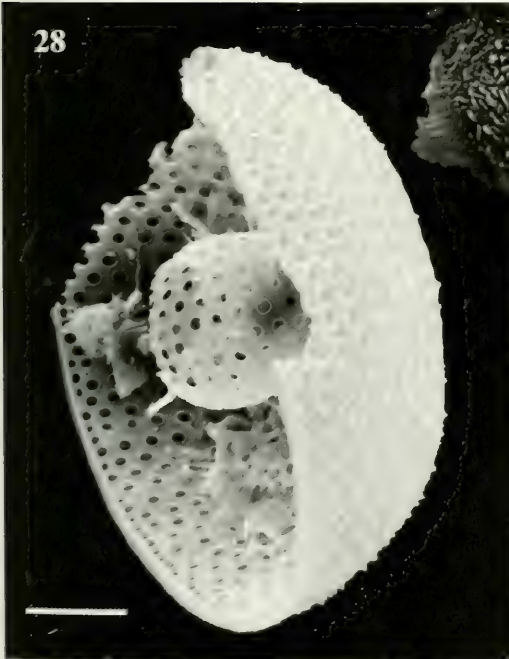
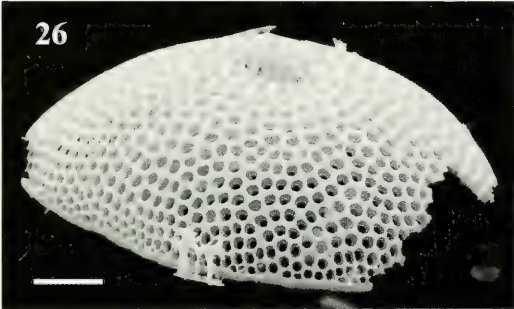
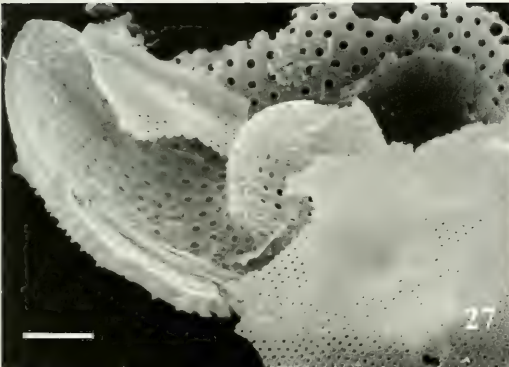
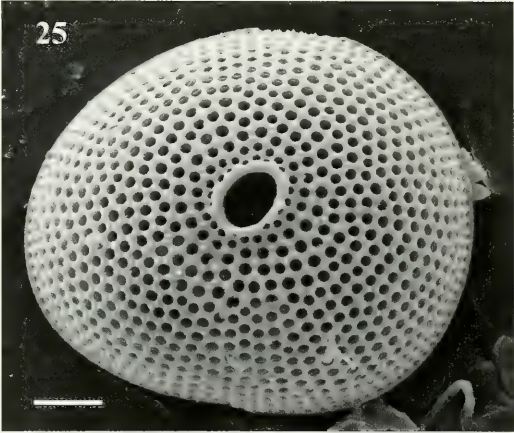
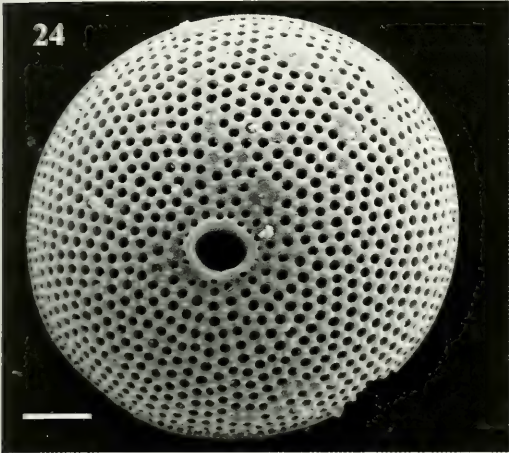




### PLATE 3

Scanning electron microscopy (SEM). **Figures 24–30. *Porodiscus splendidus* Greville.** Figures 24–26. External views. Figure 24. CAS 611226 (Chimborazo). Figure 25. CAS 711174 (Joe's River). Figure 26. CAS 611193 (Springfield). Figures 27–30. Internal views. Figures 27,28. Internal "sack". CAS (611193) Springfield. Figure 29. Broken "sack". Figure 30. Broken valve. Figures 29–30. CAS 611174 (Joe's River).

Scale bars = 10  $\mu\text{m}$ .

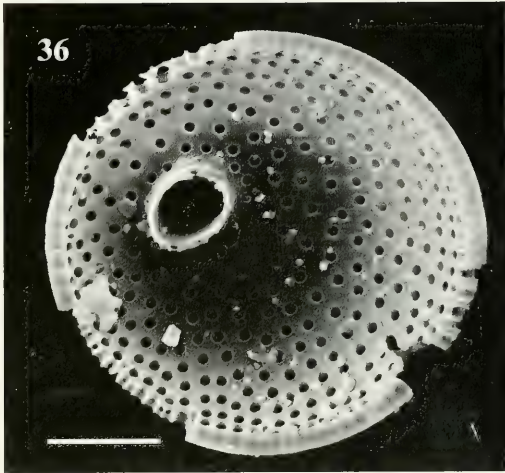
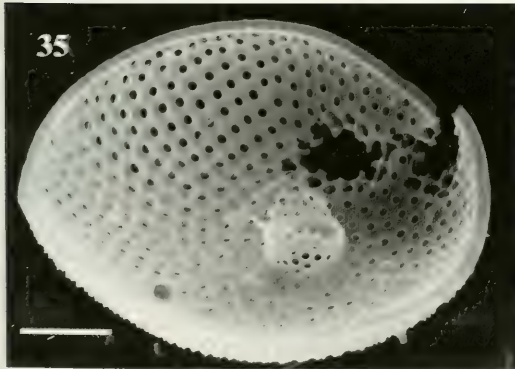
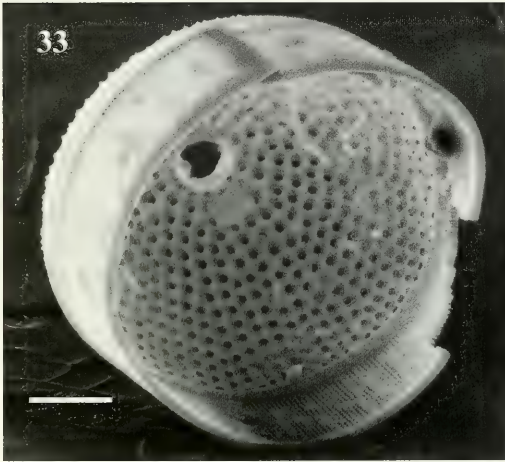
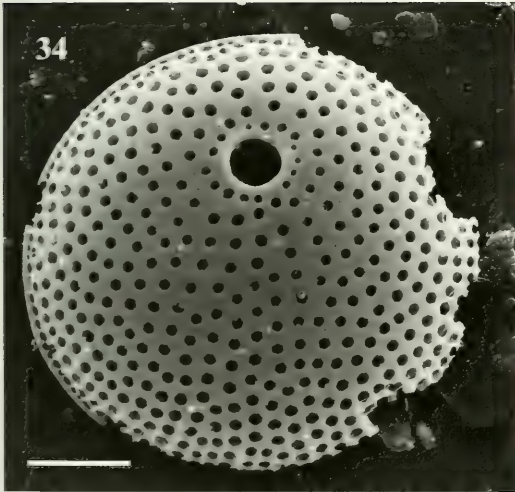
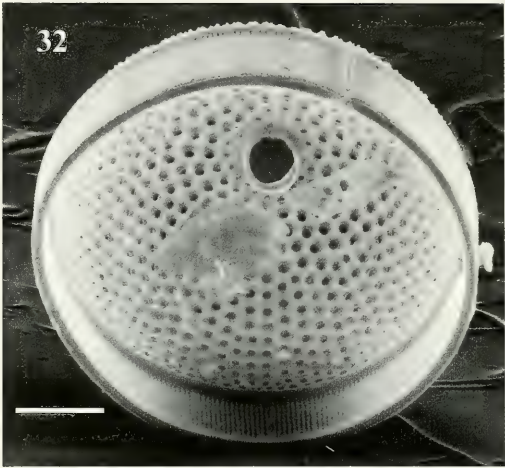
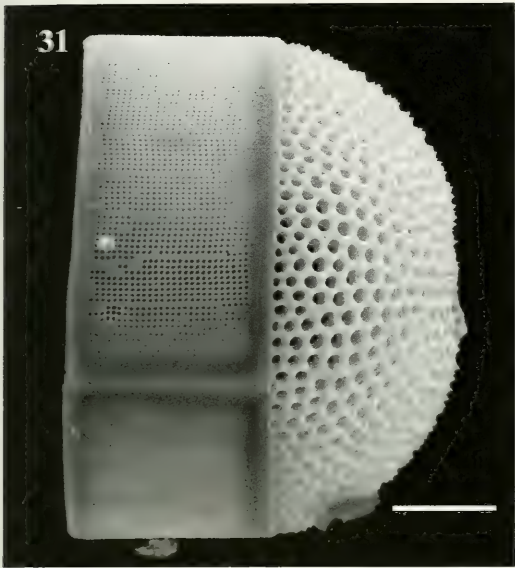


## PLATE 4

SEM. **Figures 31–33.** *Porodiscus splendidus* Greville. Valves with connection band. Figure 31. External view. Figures 32, 33. Internal view. CAS Joe's River 611174. **Figures 34–36.** *Porodiscus splendidus* var. *excentricus* (Olsht.) Olshtinskaya new comb. Figure 34. External view. Figures 35–36. Internal views. Figures 34, 36. Staroverovka. Figure 35. CAS 611174 (Joe's River).

Scale bars = 10  $\mu$ m.



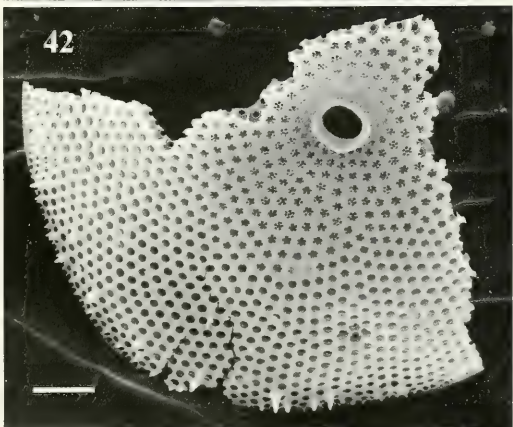
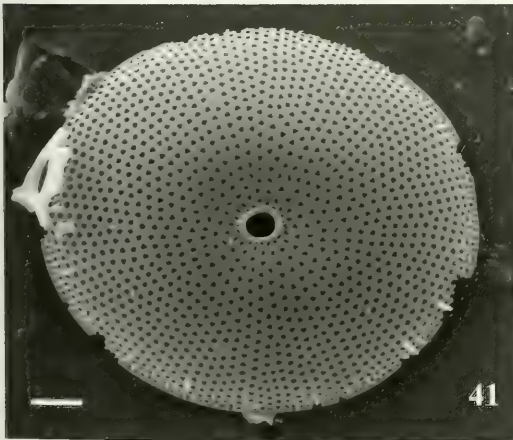
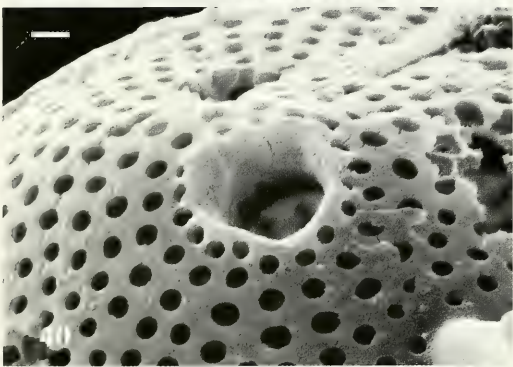
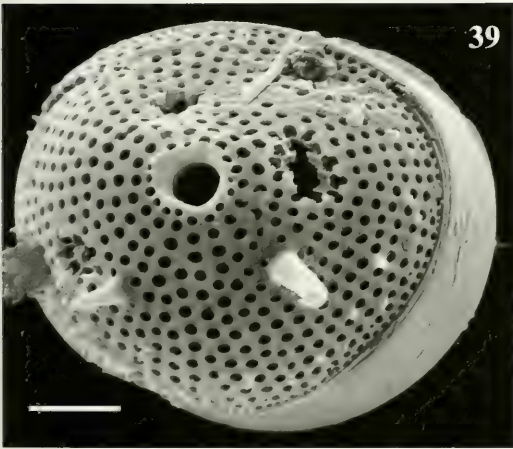
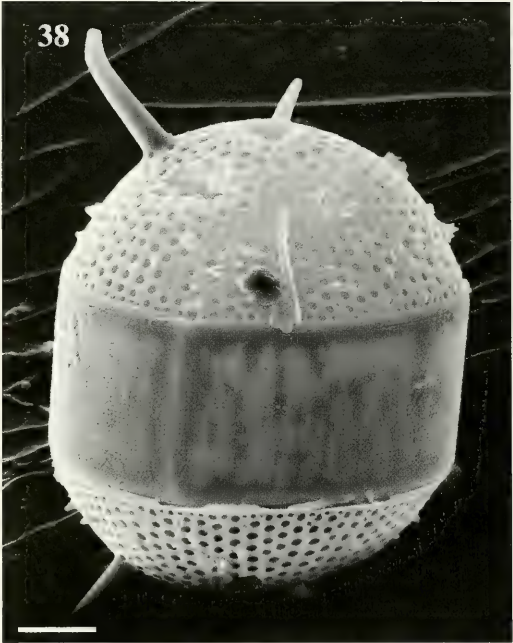
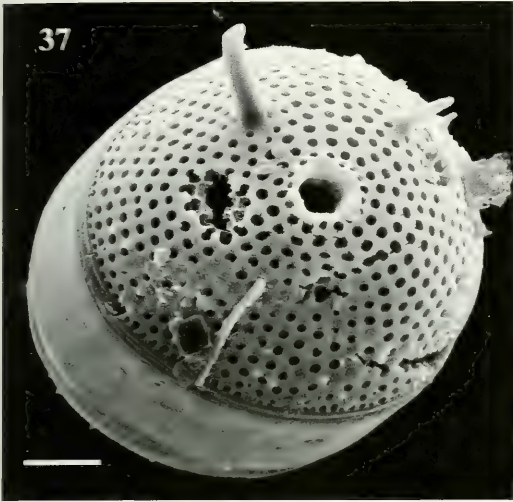


## PLATE 5

SEM. **Figures 37–40.** *Porodiscus splendidus* var. *corniger* (Greville) **Fourtanier n. comb.** Different positions of one frustule. Figure 40. “Sack” surrounded by hyaline ring. CAS 611226 (Chimborazo). **Figures 41–42.** *Porodiscus nitidus* Greville. External views; valves with spines. CAS 611174 (Joe’s River).

Scale bars = 2  $\mu\text{m}$  (Figure 40), 10  $\mu\text{m}$  (Figures 37–39, 41–42).



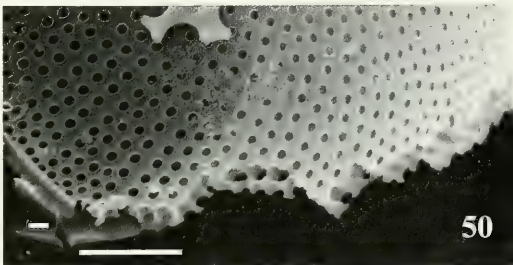
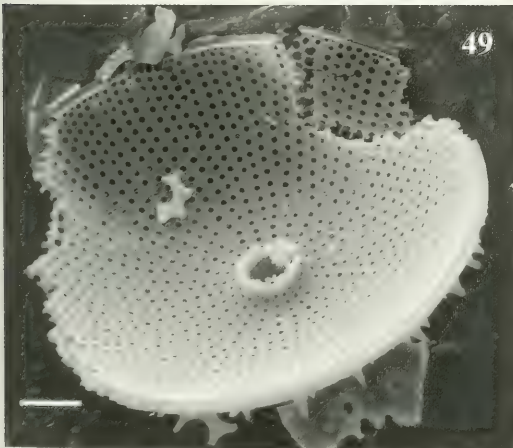
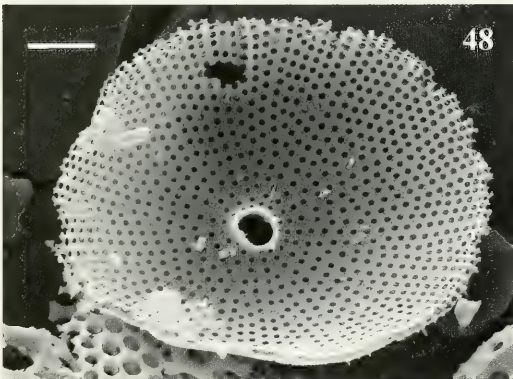
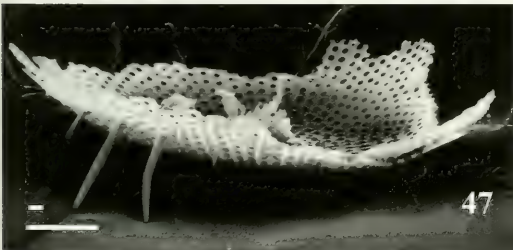
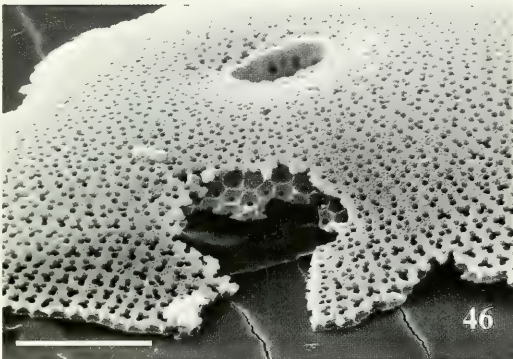
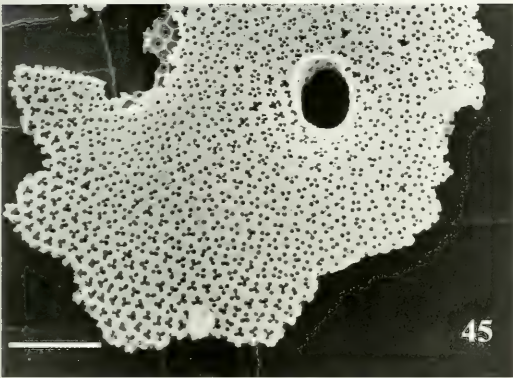
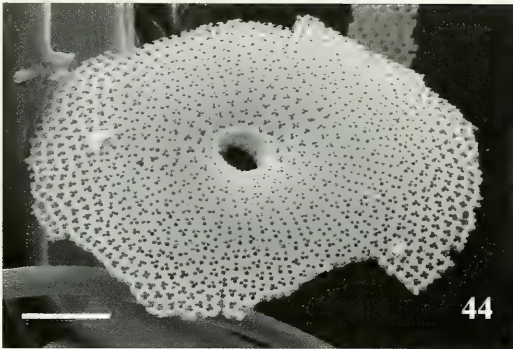
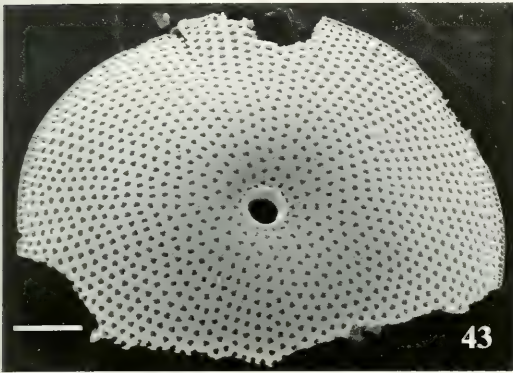




## PLATE 6

SEM. **Figures 43–50.** *Porodiscus nitidus* Greville. Figures 43–46. External views. Valves with velum. Figures 47–50. Internal views. Figures 43–44. Valves without spines. Figures 47, 49. Valves with spines. Figure 49. Rimoportulae at the ends of hyaline lines. Figures 44, 46. CAS 611226 (Chimborazo). Figures 45–50. CAS 611174 (Joe's River).

Scale bars = 10  $\mu\text{m}$ .

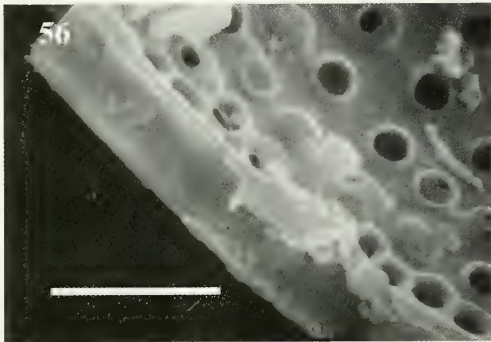
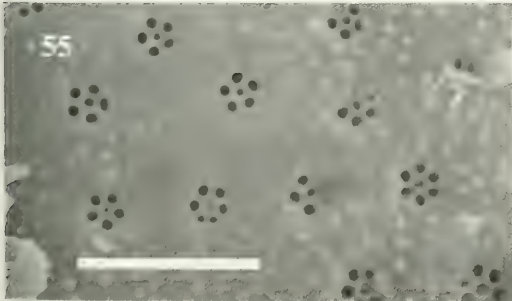
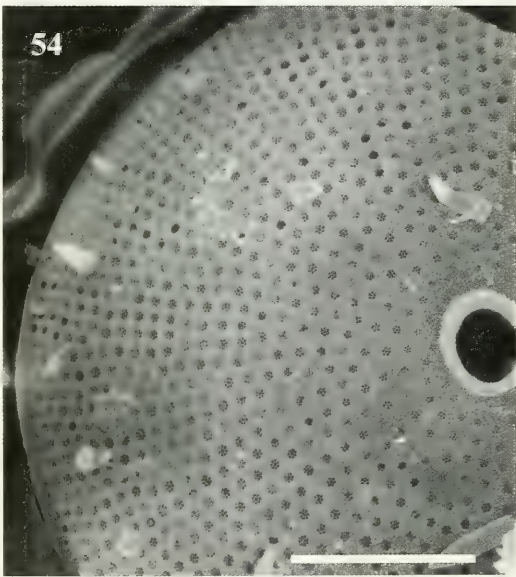
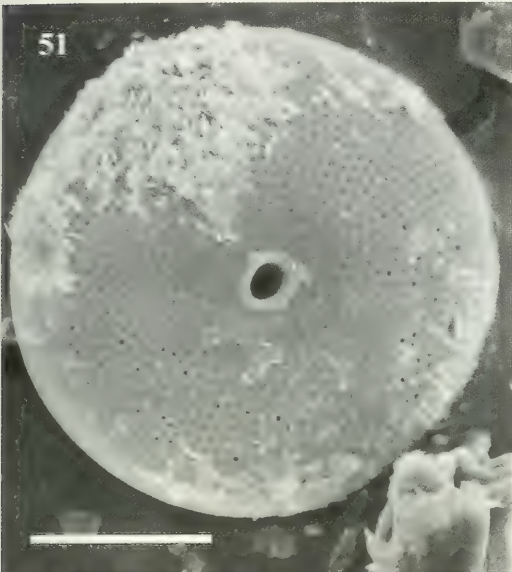


## PLATE 7

SEM. **Figures 51–56.** *Porodiscus nitidus* Greville. CAS 624819, Tasman Sea, DSDP Sample 206-16-5, 111–113 cm. Figures 51–55. External views. Figures 51, 54. Valves with spines. Figure 52. “Sack” surrounded by hyaline ring. Figure 53. The bases of broken spines, rimoportulae on the margin of valve on hyaline line under the spines. Figure 55. Velum. Figure 56. Internal view, rimoportulae.

Scale bars = 25  $\mu\text{m}$  (Figure 51), 15  $\mu\text{m}$  (Figure 54), 6  $\mu\text{m}$  (Figure 53), 4  $\mu\text{m}$  (Figure 52), 3  $\mu\text{m}$  (Figures 55–56).



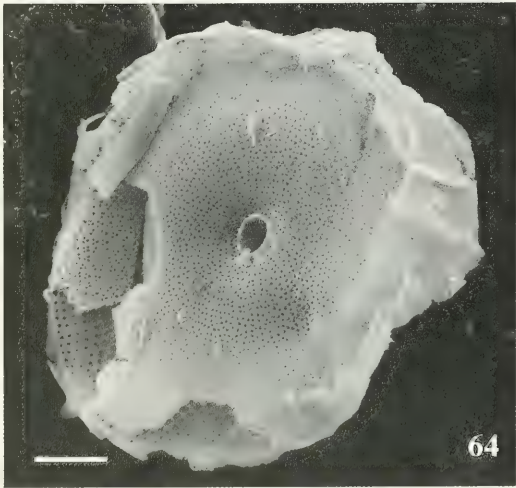
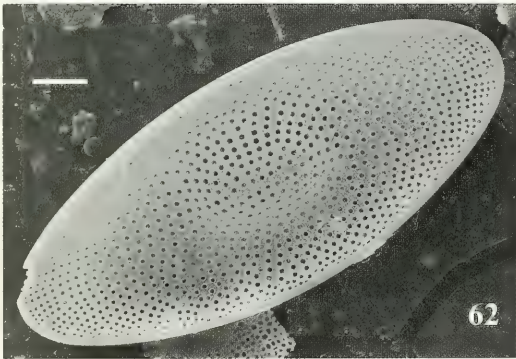
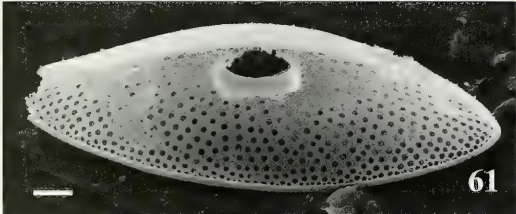
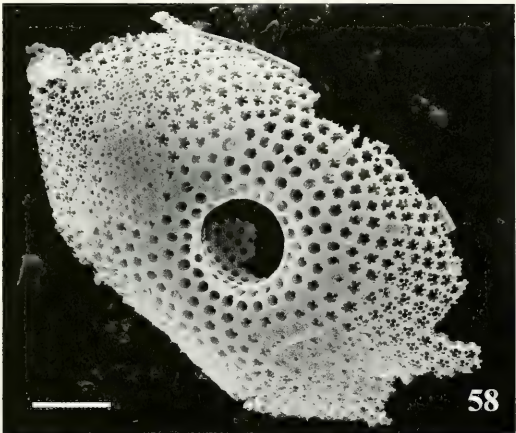
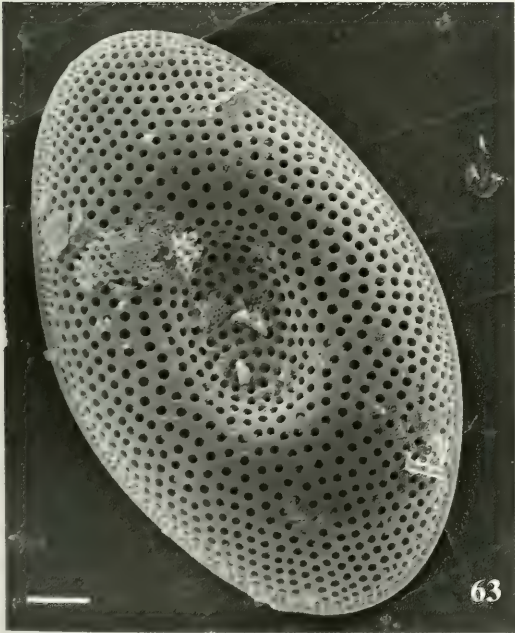
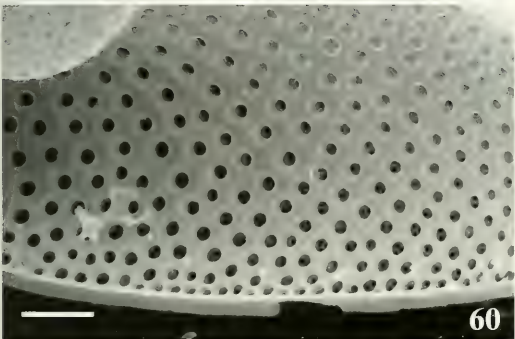
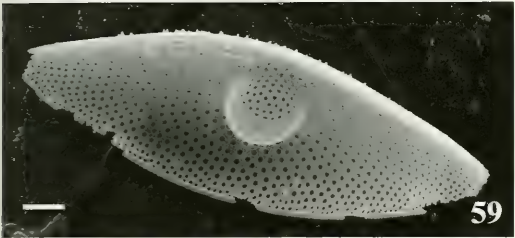
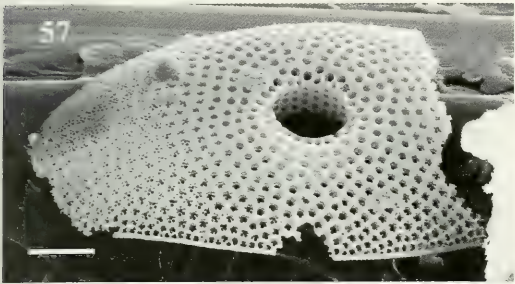


## PLATE 8

SEM. **Figures 57–61. *Porodiscus oblongus* Greville.** CAS 611193 (Springfield). Figures 57–58. External views. Velum and “sack” surrounded by hyaline ring. Figures 59–61. Internal views. Figures 59, 61. “Sack” and broken “sack.” Figure 60. Rimoportulae on the margin of valve. **Figures 62–63. *Craspedodiscus ellipticus* Gombos.** CAS 611193 (Springfield). Figure 62. Internal view. Rimoportulae on the margin of the valve. Figure 63. External view. Rimoportulae on the margin. **Figure 64. *Porodiscus conicus* Greville ?** (non-conical valve; Synonym: *Porodiscus elegans* Greville.) CAS 611235 (Chimborazo).

Scale bars = 5  $\mu\text{m}$  (Figure 60), 10  $\mu\text{m}$  (Figures 58–59, 61–63)



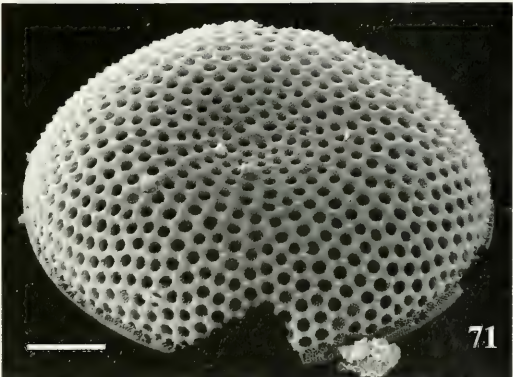
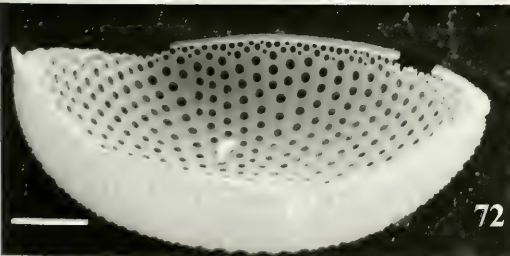
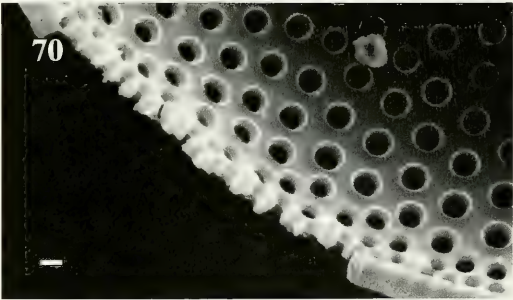
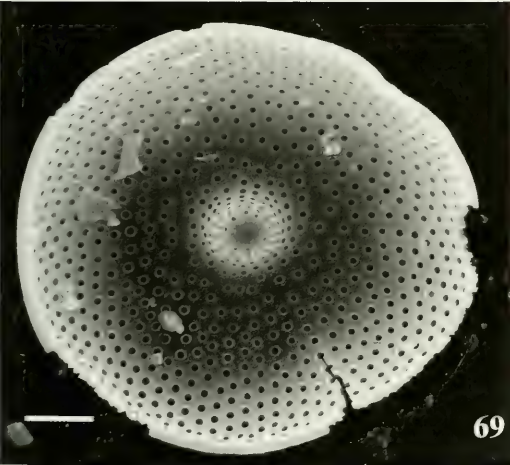
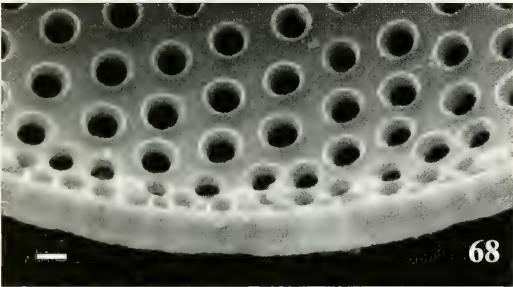
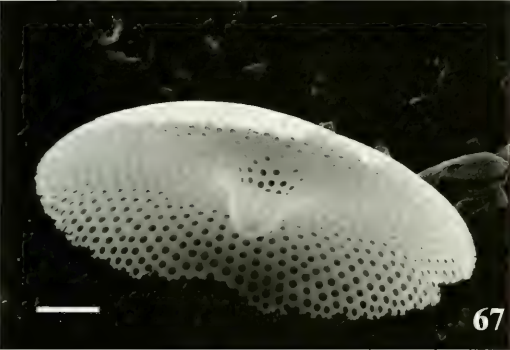
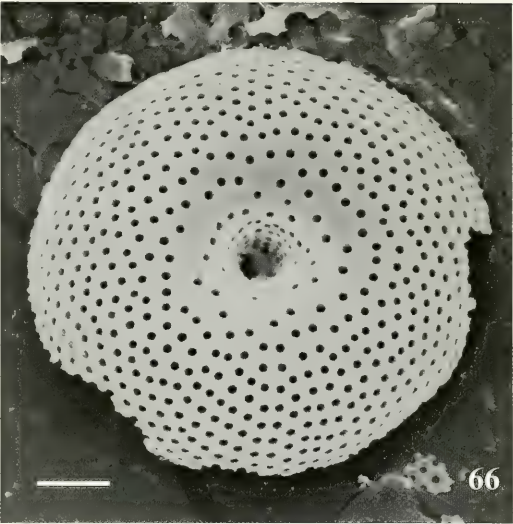
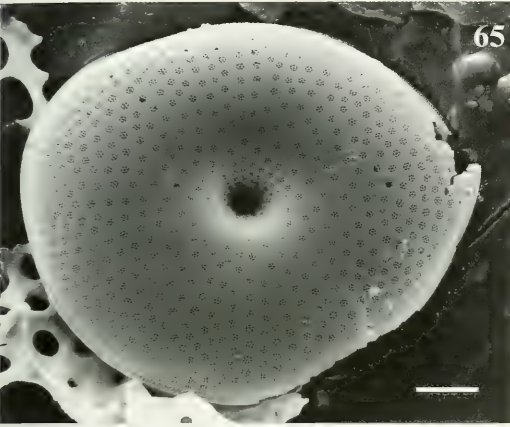




## PLATE 9

SEM. **Figures 65–70.** *Craspedodiscus umbonatus* Greville. Figures 65–66. External views. Figure 65. Velum. Figures 67–70. Internal views. Figures 67, 69. “Sack”. Figures 68, 70. Rimoportulae on the valve margin. **Figures 71–72.** *Coscinodiscus* sp. Figure 71. External view. Figure 72. Internal view. Rimoportulae on the valve margin. Figures 65–72. CAS 611174 (Joe’s River).

Scale bars = 1  $\mu\text{m}$  (Figures 68, 70), 10  $\mu\text{m}$  (Figures 65–67, 69, 71–72)

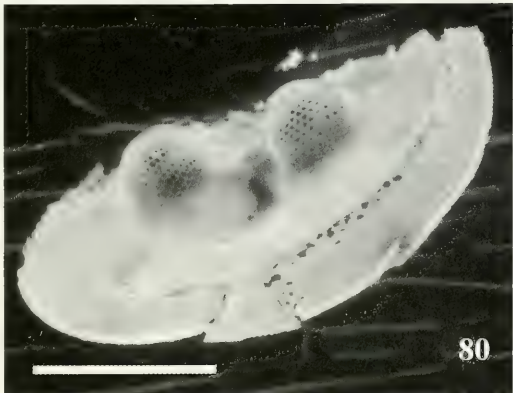
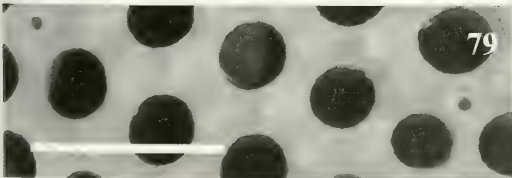
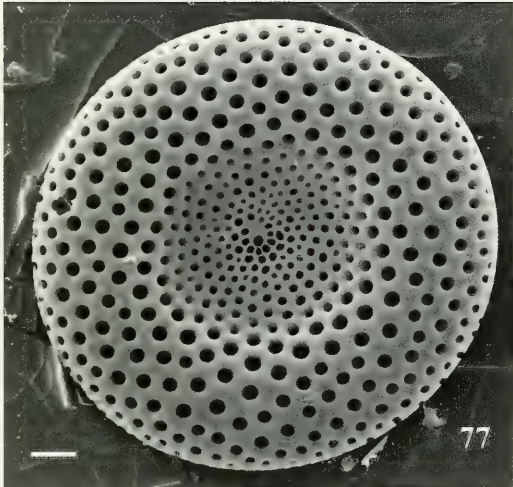
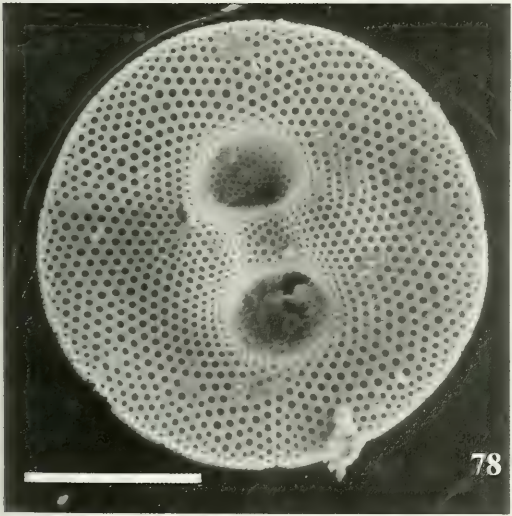
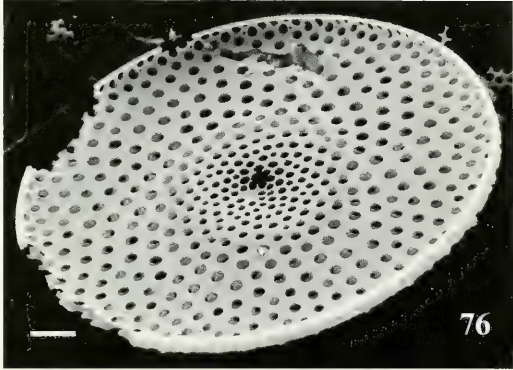
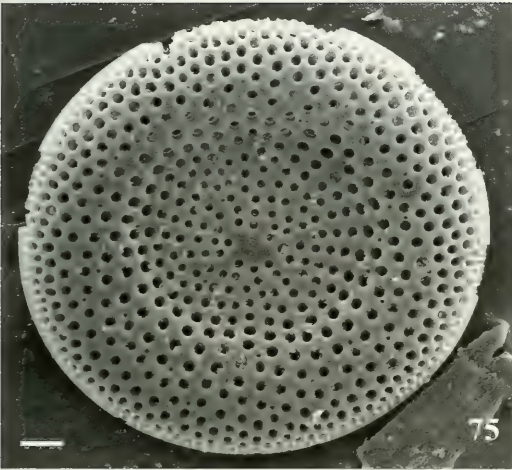
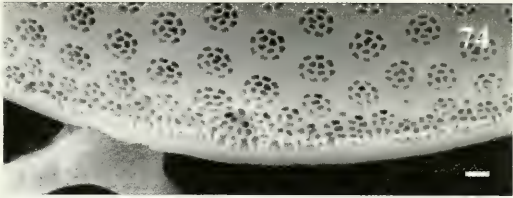
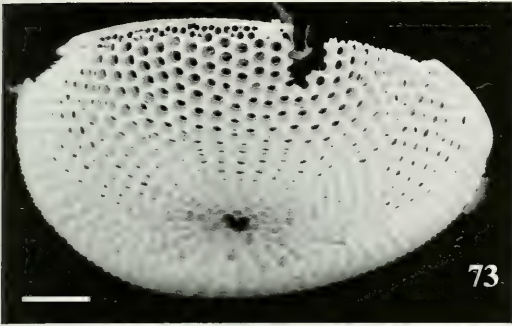


## PLATE 10

SEM. **Figure 73.** *Coscinodiscus* sp. External view. **Figure 74.** *Craspedodiscus umbonatus* Greville. Rimoportulae on the margin. Figures 73–74. CAS 611174 (Joe's River). **Figure 75.** *Coscinodiscus radiatus* Ehrenberg with slightly depressed center and rimoportulae on the valve face. Staroverivka (CAS 624820). **Figures 76–77.** *Craspedodiscus barronii* Bukry. Figure 76. Internal view. Rimoportulae on the margin. Figure 77. External view. Depressed center. CAS 611226 (Chimborazo). **Figures 78–80.** *Coscinodiscus excavatus* Greville. Figures 78–79. External view. Figure 79. Separate rimoportulae on the valve. Figure 80. Internal view. CAS 618793. Barbados, lower Oligocene.

Scale bars = 1  $\mu\text{m}$  (Figure 74), 10  $\mu\text{m}$  (Figures 73, 75–77), 7  $\mu\text{m}$  (Figure 79), 60  $\mu\text{m}$  (Figures 78, 80)



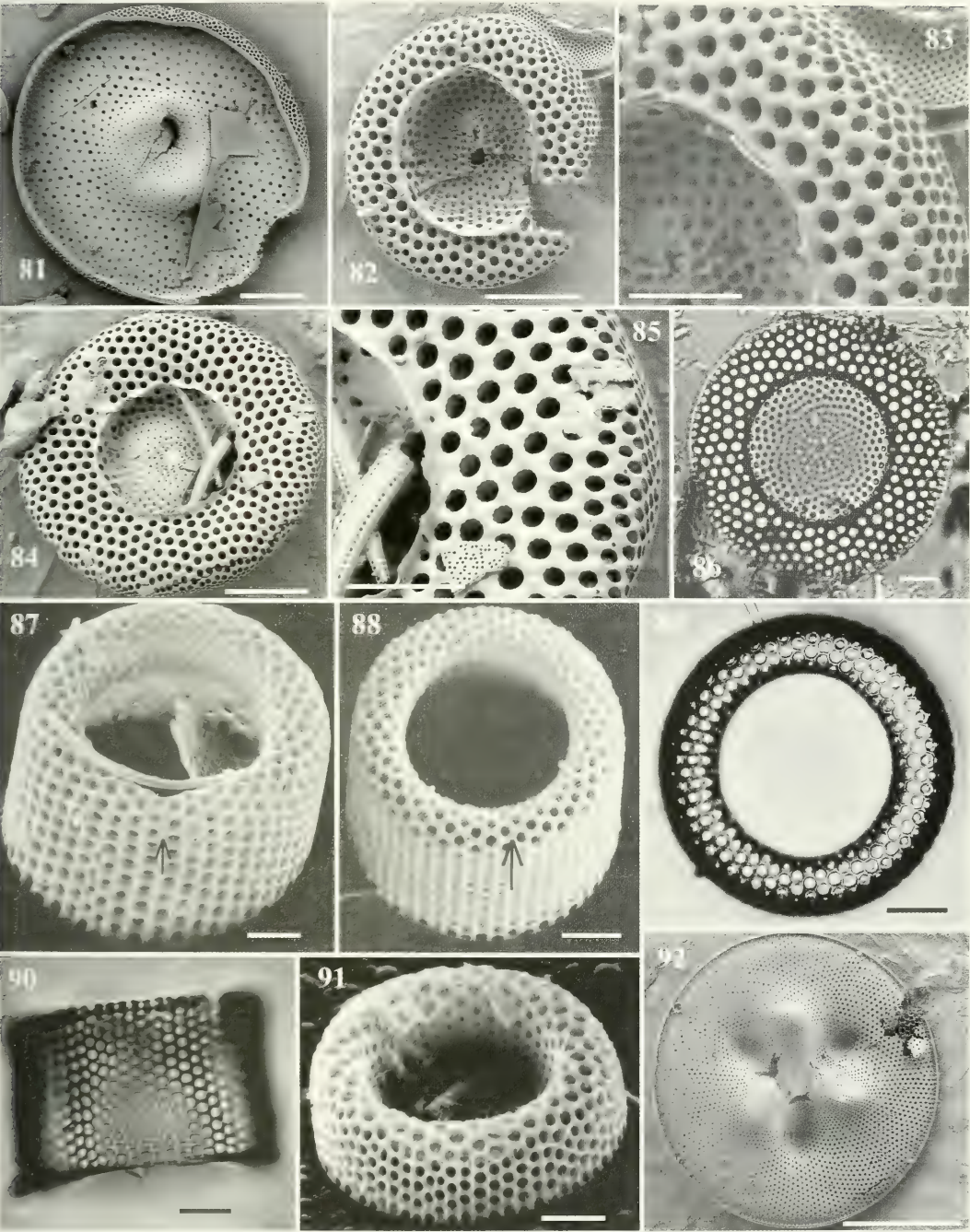


## PLATE 11

**Figures 81–86.** *Craspedodiscus coscinodiscus* Ehrenberg. (CAS 621025, Trinidad). Figure 81. Internal view. Figures 82–85. External view. Figures 81–85. SEM. Figure 86. LM. **Figure 87.** *Annellus californicus* var. *hannai* Barron. Holotype USNM 304194, sample Mf5208, southern California Continental Borderland. SEM. **Figures 88–90.** *Annellus californicus* var. *californicus* Tempère. Figures 88–89. Valve view. Figure 90. Mantle view. Sample Mf 5192, southern California Continental Borderland. Figure 88. SEM. Fig 89. 90. LM. **Figure 91.** *Craspedodiscus rhydei* Barron. DSDP 77B-28-2, 28–30 cm. SEM. **Figure 92.** *Coscinodiscus excavatus* Greville. Inside view. SEM (CAS 621025, Trinidad).

Scale bars = 20  $\mu\text{m}$  (Figures 81–82, 84), 10  $\mu\text{m}$  (Figures 83, 85–91), 100  $\mu\text{m}$  (Figure 92)







***Mesodictyopsis* Khursevich, Iwashita, Kociolek and Fedenya**  
**A New Genus of Diatoms in the Class Coscinodiscophyceae**  
**(Bacillariophyta) from Upper Miocene Sediments of Lake Baikal, Siberia**

**G.K. Khursevich<sup>1,2</sup>, J.P. Kociolek<sup>3</sup>, T. Iwashita<sup>4</sup>, S.A. Fedenya<sup>1</sup>,  
 M.I. Kuzmin<sup>5</sup>, T. Kawai<sup>6</sup>, D.F. Williams<sup>2</sup>, E.B. Karabanov<sup>2,5</sup>,  
 A.A. Prokopenko<sup>2,7</sup>, and K. Minoura<sup>4</sup>**

<sup>1</sup> Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk 220141, Republic of Belarus; Email: khurs@ns.igs.ac.by. <sup>2</sup> Baikal Drilling Project, Department of Geological Sciences, University of South Carolina, Columbia, SC 29208, USA. <sup>3</sup> Diatom Collection, California Academy of Sciences, 875 Howard Street, San Francisco, California 94103, USA. <sup>4</sup> Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Sendai 980, Japan. <sup>5</sup> Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk 664033, Russia. <sup>6</sup> National Institute for Environmental Studies, Tsukuba 305, Japan. <sup>7</sup> United Institute of Geology, Geophysics and Mineralogy, Siberian Branch of Russian Academy of Sciences, Novosibirsk 630090, Russia

A new freshwater genus *Mesodictyopsis*, studied with light (LM) and scanning electron microscopy (SEM), has been distinguished in the class Coscinodiscophyceae (Bacillariophyta) from Upper Miocene sediments of Lake Baikal. It is diagnosed by a combination of the following morphological features: a) location of the areola cribrum inside the loculus; b) arrangement of areolae on the valve face in uniseriate striae or in narrow or broad fascicles subdivided by hyaline strips or costae; c) various positions of rimoportula(e) on the valve surface; d) presence of marginal fuloportulae with three satellite pores; e) presence of valve face fuloportulae. Six new species are described. Another species, *Stephanodiscus dzhilindus* Khursevich, from the Dzhilinda basin of the Transbaikal area, appears to also share these same features. We propose to transfer this species to *Mesodictyopsis*. *Mesodictyopsis* is distinguished from its close ally, *Mesodictyon* Theriot and Bradbury, in the structure and placement of fuloportulae and position of rimoportula(e).

**Key words:** Bacillariophyta, Coscinodiscophyceae, diatoms, new genus, *Mesodictyopsis*, Late Miocene, Lake Baikal.

Lacustrine sediments of long continuous sections from Lake Baikal are important archives for studying the evolution of freshwater centric diatoms. Plio-Pleistocene diatom succession is well documented in the sedimentary record of Lake Baikal from BDP 96-1 and BDP 96-2 cores (Grachev et al. 1998; Khursevich et al. 1998, 2000, 2001a–c). The above-mentioned sections, as well as the new 600-m long drill core BDP-98, have recovered a continuous diatom record of the past 10 Ma (BDP-Members 2000) and show that the Pleistocene time interval is characterized by active speciation within the genus *Stephanodiscus* Ehrenberg. The Pliocene epoch is distinguished by the appearance, speciation and extinction of the genus *Stephanopsis* Khursevich & Fedenya. The Late Miocene differs by the appearance, speciation and extinction of a group of species whose

features do not allow placement into any previously described genus. The description of this new diatom genus, *Mesodictyopsis*, including six species from the Upper Miocene deposits of Lake Baikal, is given in the present report

## MATERIALS AND METHODS

The 600 m long borehole BDP-98 was drilled by the Russian company "Nedra Enterprise" during winter 1998 using the Baikal-2000 drilling complex placed on a barge. The drilling was performed on the Academician Ridge of Lake Baikal at 53°44'48" N and 108°24'34" E in water depth of 333 m. Continuous samples were collected to a depth of 600 m. Total core recovery was over 95%. Sediments consist of alternating biogenic diatomaceous ooze and terrigenous clay intervals. The age model for the BDP-98 section is based on the correlation of event/reversal boundaries with the reference polarity time scale (Cande and Kent 1995). Proceeding from paleomagnetic investigations and analysis of the Earth's orbital frequencies in the climatic record of the core, the sediments at a depth of 600 m have a preliminary date of 10.3 Ma (BDP-Members 2000). The Upper Miocene deposits occur in the BDP-98 core at the depth interval between approximately 600 and 221 m according to the preliminary age model for this core.

Permanent diatom slides were prepared with identical volumes of material according to the method described in Grachev *et al.* (1997). Diatoms were enumerated along vertical and horizontal transects of permanent slides in 50 or 200 fields of view depending upon diatom concentration. The distributions of total diatoms, as well as of dominant individual planktonic diatom genera including *Mesodictyopsis*, were quantitatively determined for the interval of core depth between 600 and 221 m. Elsewhere, ranked abundances (mln valves per gram of dry sediments) were used. Specimens were examined using oil immersion light microscopy (Ergaval brightfield, NA=1.25 in IGS, Belarus; DMRB with DIC optics, NA=1.4 in CAS) and scanning electron microscopy (JEOL JSM-35C in IGS, Belarus and JEOL JSM-6330F in IGPS, Sendai, Japan). To describe the new fossil diatom species, the terminology recommended by Ross *et al.* (1979) was used. The structural elements on the valve were measured using the procedure of Anonymous (1975) on not less than 30 complete diatom valves of each new taxon.

## RESULTS

### Genus *Mesodictyopsis* Khursevich, Iwashita, Kocielek, and Fedenya, gen. nov.

**DESCRIPTION:** Frustules low-cylindrical with few intercalary bands. Valves circular, 3.0–91.5  $\mu\text{m}$  in diameter, more or less flat; occasionally the central area is markedly concave or convex. Areolae loculate, having a cribrum on the inside of each loculus and a foramen on both the internal and external valve surfaces. Areolae arranged in radial rows of unequal length or in narrow or broad fascicles divided by hyaline strips or costae. Mantle not separated from the valve face by a sharp angle, but curved outwards; 1–5  $\mu\text{m}$  in wide, with areolae closer and smaller than those on the valve face; the outermost row of areolae larger. On the valve surface one rimoportula, occupying various positions (at the center, near the center, in the submarginal zone of the valve face, on the valve face/mantle junction or on the mantle) or several rimoportulae (up to 7) forming a ring on the boundary between the valve face and mantle. Internal opening of the rimoportulae is a slightly raised slit; external opening is a pore or small tube. Fultoportulae on the valve face with three, rarely two or four, satellite pores internally, represented by small external apertures. Marginal fultoportulae with three satellite pores on the internal valve surface, appearing as small openings or tubes at the base of hyaline strips externally. A ring of spines is almost always present at the valve face/mantle junction.

**TYPE SPECIES.**— *Mesodictyopsis academicus* Khursevich, Iwashita, Kociolek, and Fedenya, sp. nov.

**TYPE LOCALITY.**— The underwater Academician Ridge of Lake Baikal, Russia, borehole BDP-98 (53°44'48"N; 108°24'34"E). Abundant in the Upper Miocene deposits.

**COMMENTS.**— The new genus differs from *Mesodictyon* Theriot and Bradbury (Theriot and Bradbury 1987) in several aspects. The medial velum of *Mesodictyopsis* (a clean siliceous plate within loculate areola) is of a type different from that seen in *Mesodictyon* (a distinct medial cribrum in areola in *Mesodictyon*). In *Mesodictyopsis*, the position of rimoportulae is highly variable, while in *Mesodictyon* the rimoportula is always found on the valve mantle, behind the marginal fuloportula internally. *Mesodictyon* is known to have occurred from 12–11 Ma to 7 Ma in the western USA, Peru, France, Bulgaria, Belarus, and in Lake Baikal (*Mesodictyon nativus* has the age range ca. up to 6.5 Ma). *Mesodictyopsis* is endemic to Lake Baikal region with the age range from ca. 7–5.1 Ma (the end of Late Miocene–earliest Pliocene). In Lake Baikal there is a long, continuous sedimentary record where there are several endemic freshwater centric diatom genera (*Concentrodiscus*, *Stephanopsis*) which replace each other from bottom to top and have some common inherited morphological features (such as the various inconstant position of rimoportula on the valve surface including some taxa with the location of rimoportulae in or near the center of the valve). This situation is wanting in *Mesodictyon* species. Lake Baikal has very high levels of endemism, not only of species, but also genera (among many organisms including diatoms). The extinct endemic genera *Mesodictyopsis* and *Stephanopsis*, for example, have marginal fuloportulae with three satellite pores and the valve face fuloportulae with three satellite pores. We know many closely related centric genera with external cribra (*Actinocyclus*, *Cestodiscus*, *Cosmiodiscus* and others), many genera with internal cribra (*Thalassiosira*, *Concentrodiscus*, *Stephanodiscus* and others), and now we recognize several genera with a medial velum.

We have recognized six new species in this genus; these are described below.

***Mesodictyopsis academicus* Khursevich, Iwashita, Kociolek, and Fedenya, sp. nov.**

(Plate 1, Figs 1–3, 6; Plate 2, Figs 1–6. Plate 1, figure 1 is of the holotype.)

**DESCRIPTION.**— Valves circular, 9.5–50.0  $\mu\text{m}$  in diameter. Areolae 10–25 in 10  $\mu\text{m}$  along the valve radius, arranged in radial, uniseriate striae or extending from the center and becoming bi- or triseriate fascicles in the submarginal zone of the valve face. Hyaline strips or costae divide uniseriate striae or fascicles from each other and continue from the valve face to the mantle, (6)8–16 in 10  $\mu\text{m}$ . A single rimoportula, usually positioned in the valve center or near the center. Valve face fuloportulae, 2–14, each with three satellite pores, situated within the central area in radial areolar rows replacing 1–4 areolae per row. Valve mantle (up to 2  $\mu\text{m}$  in height) with 2–5 small areolae in a vertical row, with 36–40 rows of areolae in 10  $\mu\text{m}$ . Marginal fuloportulae with three satellite pores, (6)8–16 in 10  $\mu\text{m}$ , located at the base of each hyaline strip, rarely every second or third one. A ring of irregularly located spines may be present at the valve face/mantle junction.

**HOLOTYPE.**— Slide No. 3495a, BDP-98, core 198-1 (18 cm), deposited at the Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk, Belarus.

**ISOTYPE.**— Slide No. 3495b, BDP-98, core 198-1 (18 cm), deposited at the Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia.

**TYPE MATERIAL.**— Housed in the G. K Khursevich Collection at the Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk, Belarus; Baikal Drilling Project Collection, Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia, and in Diatom Collection, California Academy of Sciences, San Francisco, USA.



**TYPE LOCALITY.**— The underwater Academician Ridge of Lake Baikal, Russia, borehole BDP-98, depth 334–461 m from sediment surface.

***Mesodictyopsis medius* Khursevich and Iwashita, sp. nov.**

(Plate 1, Fig. 11; Plate 3, Figs. 1–6. Plate 1, Fig. 11 is of the holotype.)

**DESCRIPTION.**— Valves circular, more or less flat, 11.0–24.5  $\mu\text{m}$  in diameter. Areolae 14–16(20) in 10  $\mu\text{m}$  along the valve radius, arranged in radial rows of unequal length separated by hyaline strips, 14–18 in 10  $\mu\text{m}$ . A single rimoportula situated in the valve center and surrounded by a hyaline ring. Valve face fuloportulae (from 3 to 9), each with three satellite pores, form an irregular ring at a distance of  $\frac{1}{3}$ – $\frac{1}{2}$  from the valve center. Valve mantle (1–2  $\mu\text{m}$  in height) has 2–4 small areolae in a vertical row (35–40 areolar rows in 10  $\mu\text{m}$  near the edge of mantle) and a marginal ring of fuloportulae with three satellite pores, 8–12(14) in 10  $\mu\text{m}$ , located at the base of each or every second or third hyaline strip. Spines may be present at the valve face/mantle junction.

**HOLOTYPE.**— Slide No. 108616, BDP-98, core 231-1 (91 cm) deposited at the Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Sendai, Japan.

**TYPE MATERIAL.**— Housed in the IGPS Collection at the Institute of Geology and Paleontology, Graduate School of Science, Tohoku University, Sendai, Japan; Baikal Drilling Project Collection, Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia.

**TYPE LOCALITY.**— The underwater Academician Ridge of Lake Baikal, Russia, the borehole BDP-98, depth 403–424 m from sediment surface.

**COMMENTS.**— This species differs from *Mesodictyopsis academicus* by the presence of non-fasciculated striae of areolae only and valve face fuloportulae forming an irregular ring in the middle of the valve radius.

***Mesodictyopsis peculiaris* Khursevich, Kociolek, and Fedenya, sp. nov.**

(Plate 1, Fig. 13; Plate 4, Figs. 1–2. Plate 1, Fig. 13 is of the holotype.)

**DESCRIPTION.**— Valves circular, flat or slightly convex, 3.0–9.5  $\mu\text{m}$  in diameter. Areolae, up to 20 in 10  $\mu\text{m}$  along the radius, located in single radial rows divided by hyaline strips, 15–20 in 10  $\mu\text{m}$ . Not all rows of areolae reach the valve center; hence the center not densely structured. One fuloportula with two satellite pores occurs near the valve center. A single rimoportula occurs in the submarginal zone of the valve face, between two closely located marginal fuloportulae. 4–6 fuloportulae with three satellite pores on the mantle; among which two are placed close to one another, the rest widely spaced. Valve mantle shallow (up to 1  $\mu\text{m}$  high), consisting of 1–2 small areolae in a vertical row. Spines positioned at every hyaline strip at the valve face/mantle junction; often broken.

**HOLOTYPE.**— Slide No. 3495a, BDP-98, core 198-1 (18 cm), deposited at the Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk, Belarus.

**ISOTYPE.**— Slide No. 3495b, BDP-98, core 198-1 (18 cm), deposited at the Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia.

**TYPE MATERIAL.**— Housed in the G.K. Khursevich Collection at the Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk, Belarus; Baikal Drilling Project Collection, Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia, and in Diatom Collection, California Academy of Sciences, San Francisco, USA.

**TYPE LOCALITY.**— The underwater Academician Ridge of Lake Baikal, Russia, borehole BDP-98, depth 328–377 m from sediment surface.

*Comments:* This species differs from *Mesodictyopsis medius* by the smaller size of valves, as well as the specific location of a single rimoportula and marginal fultoportulae on the valve surface.

***Mesodictyopsis singularis* Khursevich, Iwashita, and Fedenya, sp. nov.**

(Plate 1, Figs. 7, 10, 14–15; Plate 4, Figs. 3–5. Plate 1, Fig. 7 is of the holotype.)

**DESCRIPTION.**— Valves circular, more or less flat, 4.0–17.2  $\mu\text{m}$  in diameter. Areolae 12–16 (20) in 10  $\mu\text{m}$  along the radius, grouped in uniseriate radial striae of unequal length, separated by hyaline strips, 14–18 in 10  $\mu\text{m}$ . One–several fultoportulae, each with three satellite pores, found near the valve center. A single rimoportula occurs just inside the ring of marginal fultoportulae. Marginal fultoportulae with three satellite pores, (6)8–10 in 10  $\mu\text{m}$ , located at the base of each or every second, rarely every third hyaline strip on the mantle. Valve mantle (up to 1  $\mu\text{m}$  high) perforated by 1–3 small areolae in a vertical row (up to 40 rows of areolae in 10  $\mu\text{m}$ ). Small pointed spines usually present at every hyaline strip on the boundary between the valve face and mantle.

**HOLOTYPE.**— Slide No. 3040a, BDP-98, core 174-1 (68 cm), deposited at the Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk, Belarus.

**ISOTYPE.**— Slide No. 3040b, BDP-98, core 174-1 (68 cm), deposited at the Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia.

**TYPE MATERIAL.**— Housed in the G.K. Khursevich Collection at the Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk, Belarus, and Baikal Drilling Project Collection, Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia.

**TYPE LOCALITY.**— The underwater Academician Ridge of Lake Baikal, Russia, borehole BDP-98, depth 304–452 m from sediment surface.

**COMMENTS.**— This species differs from *Mesodictyopsis peculiaris* by the more dense placement of marginal fultoportulae.

***Mesodictyopsis baicalensis* Khursevich, Iwashita, Kocielek, and Fedenya, sp. nov.**

(Plate 1, Figs. 4–5, 8, 17–18; Plate 5, Figs. 1–6, Plate 6, Figs. 1–6. Plate 1, Fig. 5 is of the holotype.)

**DESCRIPTION.**— Valves circular, with markedly concave or convex central area, 15.5–91.0  $\mu\text{m}$  in diameter. Areolae, 11–18(20) in 10  $\mu\text{m}$  along the valve radius, arranged in radial uniseriate uneven striae within the central area becoming bi- multiseriate fascicles (up to 5 areolar rows) in the submarginal zone of the valve face. Fascicles of areolae divided by hyaline strips or costae, 5–7 in 10  $\mu\text{m}$ , continuing from the valve face to the mantle. 1 to 7 valve face fultoportulae, each with three satellite pores (rarely one fultoportula may have four satellite pores), occur in the valve center or near the center replacing 1–4 areolae per row. Rimoportulae (1–7) located in the upper part of the valve mantle a little below the spine insertion; appear as short tubes, externally, and slightly raised slit oriented variously, internally. Rimoportulae may be positioned both on hyaline strips and in radial areolar rows. Valve mantle (up to 5  $\mu\text{m}$  high) with 2–8 small areolae in a vertical row (30–40 rows of areolae in 10  $\mu\text{m}$ ) and a ring of marginal fultoportulae located at the base of each or every second, rarely every third, hyaline strip. Marginal fultoportulae having three satellite pores internally and small tubes externally. Conic spines are spaced irregularly at the valve face/mantle junction.

**HOLOTYPE.**— Slide No. 2810a, BDP-98, core 150-1 (18 cm), deposited at the Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk, Belarus.

**ISOTYPE.**— Slide No. 2810b, Bdp-98, core 150-1 (18 cm), deposited at the Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia.

**TYPE MATERIAL.**— Housed in the G.K. Khursevich Collection at the Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk, Belarus; Baikal Drilling Project Collection, Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia, and in Diatom Collection, California Academy of Sciences, San Francisco, USA.

**TYPE LOCALITY.**— The underwater Academician Ridge of Lake Baikal, Russia, borehole BDP-98, depth 259–302 m from sediment surface.

**COMMENTS.**— This species differs from *Mesodictyopsis singularis* mainly by the larger size of valves, as well as by the presence of distinct areolar fascicles towards the margin of the valve face.

***Mesodictyopsis similis* Khursevich and Fedenya, sp. nov.**

(Plate 1, Figs. 9, 16; Plate 4, Figs. 6–7. Plate 1, Fig. 16 is of the holotype.)

**DESCRIPTION.**— Valves circular, flat or slightly convex, 3.5–10.0  $\mu\text{m}$  in diameter. Areolae, 15–20 in 10  $\mu\text{m}$  along the radius, arranged in short radial uniseriate striae extending from  $\frac{1}{3}$  to about  $\frac{1}{2}$  of the radius from the valve margin to the center. Hyaline strips separating uniseriate striae from each other 15–20 in 10  $\mu\text{m}$ . Central area hyaline except the presence of a single valve face fuloportula with two satellite pores. One rimoportula occurs at the same level with marginal fuloportulae having three satellite pores. Valve mantle shallow (up to 1  $\mu\text{m}$  high) with one areola placed in a vertical row. Spine occurrence and placement difficult to determine, usually broken.

**HOLOTYPE.**— Slide No. 2525a, BDP-98, core 142-1 (94 cm), deposited at the Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk, Belarus.

**ISOTYPE.**— Slide No. 2525b, BDP-98, core 142-1 (94 cm), deposited at the Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia.

**TYPE MATERIAL.**— Housed in the G.K. Khursevich Collection at the Institute of Geological Sciences, National Academy of Sciences of Belarus, Minsk, Belarus, and Baikal Drilling Project Collection, Institute of Geochemistry, Siberian Branch of Russian Academy of Sciences, Irkutsk, Russia.

**TYPE LOCALITY.**— The underwater Academician Ridge of Lake Baikal, Russia, borehole BDP-98, depth 254–304 m from sediment surface.

**COMMENTS.**— This species differs from *Mesodictyopsis peculiaris* and *M. singularis* by the different location of a single rimoportula on the valve surface.

## DISCUSSION

There are now two freshwater genera (*Mesodictyon* and *Mesodictyopsis*) of the family *Stephanodiscaceae* Makarova which have the medial cribrum within the loculate areolae. This feature is the main diagnostic character of these genera. *Mesodictyon* has no valve face fuloportulae and possesses marginal fuloportulae with two satellite pores, while *Mesodictyopsis* has not only marginal fuloportulae with three satellite pores, but also valve face fuloportulae. In addition, the rimoportula(e) is typically on the mantle outside of the ring of marginal fuloportulae in *Mesodictyon* (Theriot 1990). As far as the species of *Mesodictyopsis* are concerned, they can be separated into three morphological groups with respect to the rimoportula(e) position on the valve surface.

One morphological group of *Mesodictyopsis* is composed of species characterizing by the location of a single rimoportula at the valve face/mantle junction or in the submarginal zone of the



valve face (*M. singularis*, *M. peculiaris*). The second group is based on the placement of a single rimoportula in the valve center or near the center (*M. academicus*, *M. medius*). Finally, the third morphological group is distinguished by the position of rimoportula(e) on the valve mantle (*M. baicalensis*, *M. similis*).

In general, species of *Mesodictyopsis* were found in the sediments of BDP-98 section in the interval of depth 461–254 m. According to the preliminary age model for the BDP-98 drill core (BDP-Members 2000), the appearance, development and extinction of *Mesodictyopsis* in the ancient basin proceeded during the Late Miocene period from ~ 8.5 to 6.0 Ma.

In our opinion, the species *Stephanodiscus dzhilindus* Khursevich, which occurs in the Miocene deposits within the Dzhilinda depression of the Transbaikal area (Khursevich 1994) should also be transferred to the genus *Mesodictyopsis*. Although cribra were not observed in specimens of *Stephanodiscus dzhilindus*, presence of funnel-like areolae, marginal fultoportulae with three satellite pores and a single valve face fultoportula suggest that *Mesodictyopsis* is its best generic placement. Hence, the new combination is proposed:

***Mesodictyopsis dzhilindus* (Khursevich) Khursevich.**

**BASIONYM.**— *Stephanodiscus dzhilindus* Khursevich (Khursevich 1994: Morphology and taxonomy of some centric diatom species from the Miocene sediments of the Dzhilinda and Tunkin hollows. Pages 271–272 and fig. 3 in J.P. Kocielek, ed., *Proceedings of the 11<sup>th</sup> International Diatom Symposium*, San Francisco. Memoirs of the California Academy of Sciences no. 17).

The extinct genus *Mesodictyopsis* is characteristic both of the Upper Miocene sediments from Lake Baikal and the Transbaikal area.

#### ACKNOWLEDGMENTS

This work was supported by National Scientific Foundation of USA (NSF) grants EAR-93-1720401, EAR-96-14770 and the Siberian Branch of Russian Academy of Sciences. Cores for this study were made possible through the Baikal Drilling Project (BDP) supported by NSF and International Continental Scientific Drilling Program (ICDP), the Russian Academy of Sciences, the Russian Ministry of Geology, the Science and Technology Agency (STA) of Japan. Authors wish to express their gratitude to B.N. Khakhaev, L.A. Pevzner and V.V. Kochukov of the Nedra Drilling Enterprise for organizing and providing the deep drilling of Lake Baikal sediments. We also thank A.N. Gvozdkov and N. Soshina of the Institute of Geochemistry for technical assistance with the BDP-98 core and smear slide preparation.

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## Plate 1

### Light Microscopy

Species of *Mesodictyopsis* from the Upper Miocene sediments  
of BDP-98 drill core. Scale bar in fig. 1 = 10  $\mu$ m for all figures.

1-3, 6. *Mesodictyopsis academicus*. Fig. 1. Holotype specimen, BDP-98 core, 198-1, 18 cm.

4-5, 8, 17-18. *Mesodictyopsis baicalensis*. Fig. 5. Holotype specimen, BDP-98 core, 150-1, 18 cm.

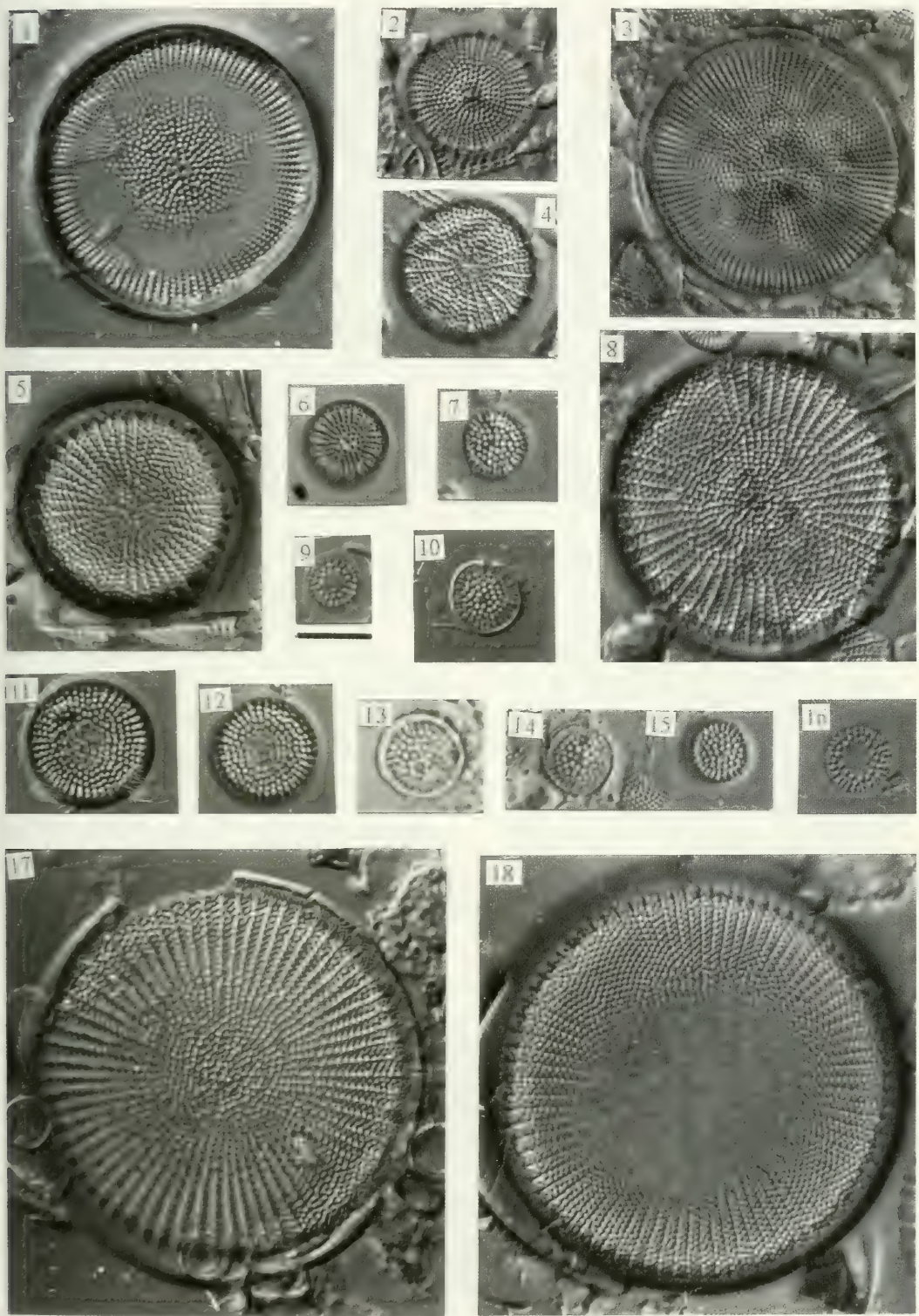
7, 10, 14-15. *Mesodictyopsis singularis*. Fig. 7. Holotype specimen, BDP-98 core, 174-1, 68 cm.

9, 16. *Mesodictyopsis similis*. Fig. 16. Holotype specimen, BDP-98 core, 142-1, 94 cm.

11-12. *Mesodictyopsis medius*. Fig. 11. Holotype specimen, BDP-98 core, 231-1, 91 cm.

13. *Mesodictyopsis peculiaris* Holotype specimen, BDP-98 core, 198-1, 18 cm.





## Plate 2

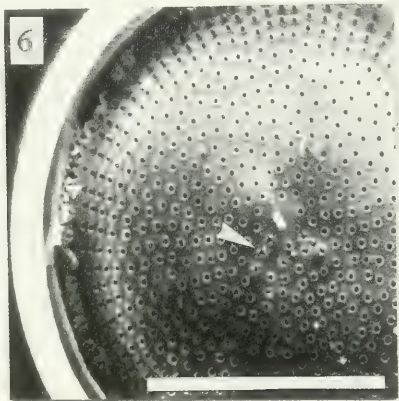
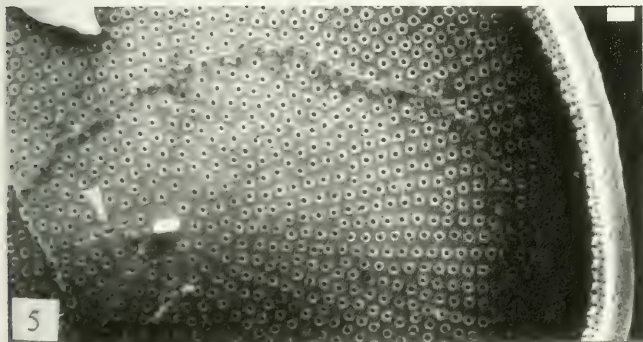
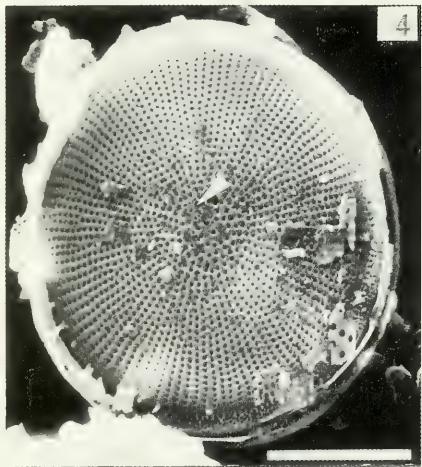
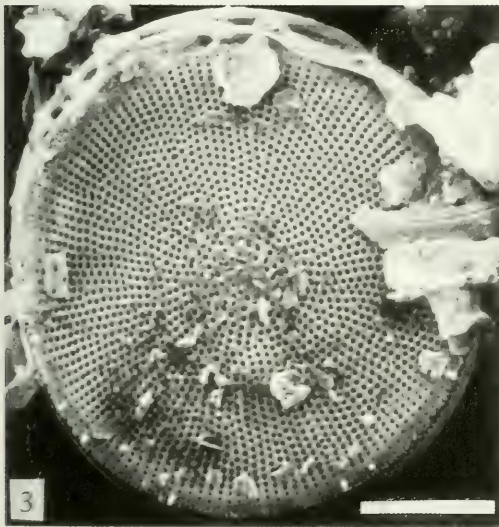
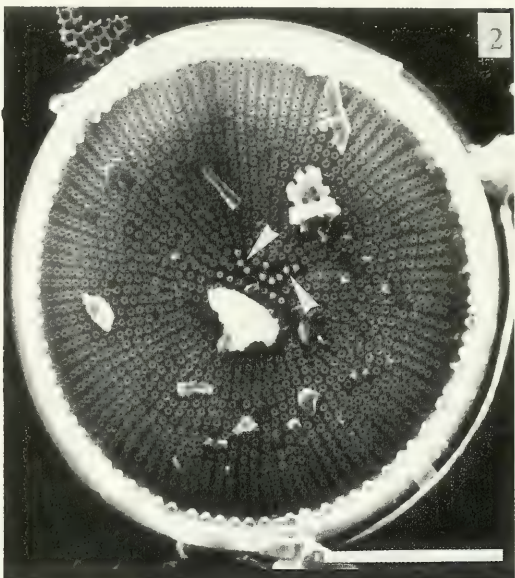
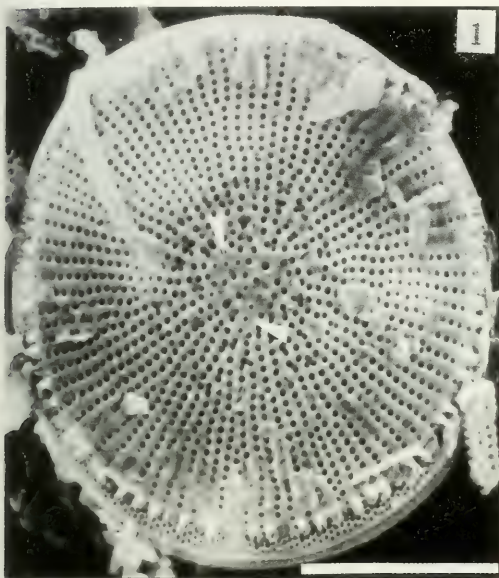
### Scanning Electron Microscopy

#### *Mesodictyopsis academicus*

Figs. 1, 3–4. External views of the valve surface with small openings of valve face fuloportulae near the valve center (arrows); scale bars = 10  $\mu\text{m}$ .

Figs. 2, 5–6. Internal views of the valve surface with a single rimoportula and valve face fuloportulae with three satellite pores near the valve center (arrows). Scale bars = 10  $\mu\text{m}$  in Figs. 2–6; scale bar = 1  $\mu\text{m}$  in Fig. 5.







## Plate 3

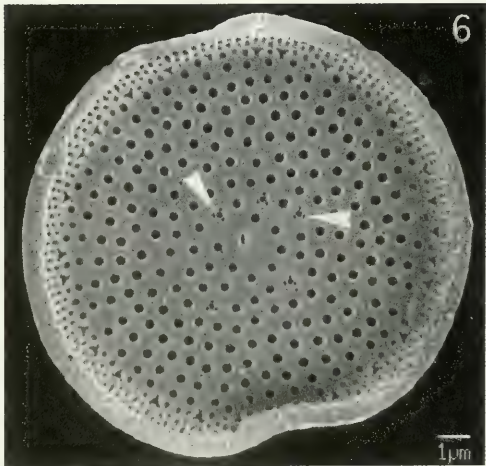
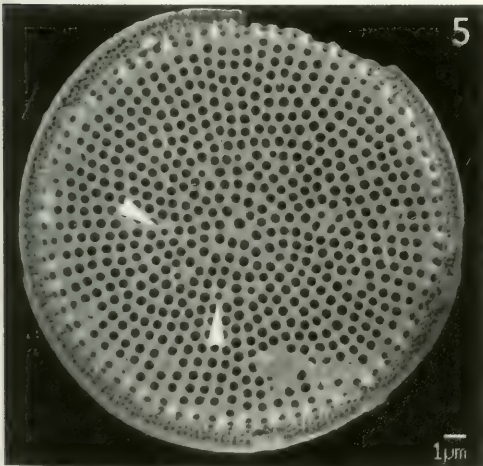
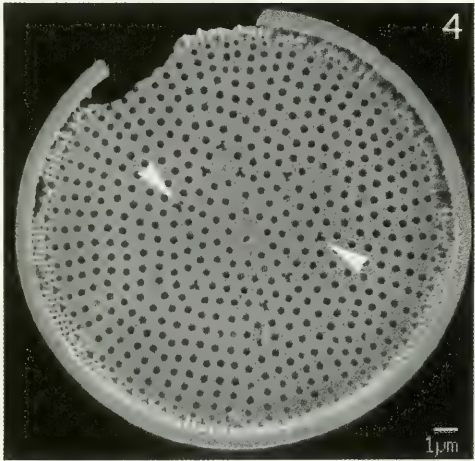
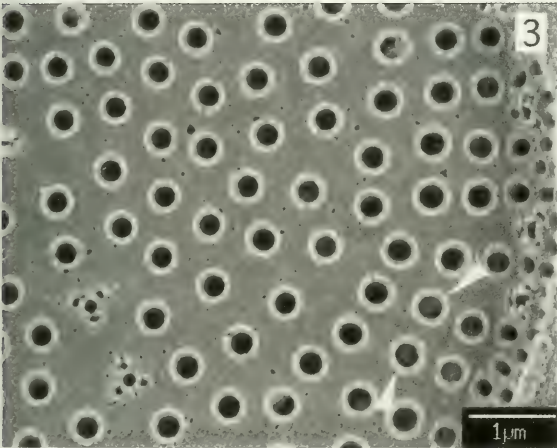
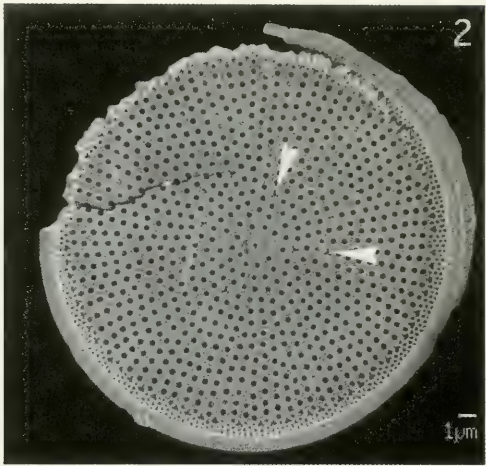
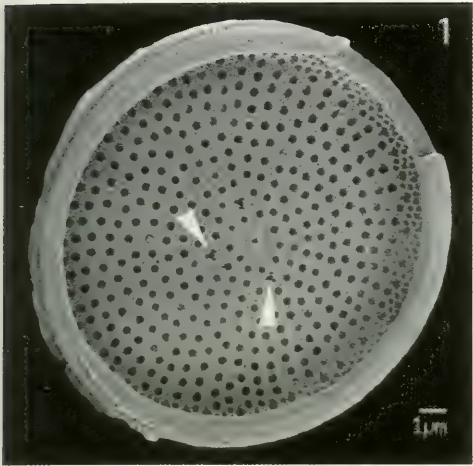
### Scanning Electron Microscopy

#### *Mesodictyopsis medius*

Figs. 1–2, 4, 6. Internal views of the valve surface with a single rimoportula in the valve center and an irregular ring of valve face fultoportulae with three satellite pores located at the distance  $\frac{1}{3}$ – $\frac{1}{2}$  from the valve center (arrows).

Fig. 3. Fragment of internal view of the valve surface with a cribrum inside of loculus (arrow).

Fig. 5. External view of the valve surface with a ring of valve face fultoportulae openings (arrows), scale bars = 1  $\mu$ m.



## Plate 4

### Scanning Electron Microscopy

#### 1-2. *Mesodictyopsis peculiaris*

1. External view of the valve surface with a single opening of the valve face fultoportula near the center (arrow); scale bar = 2  $\mu\text{m}$ .

2. Internal view of the valve surface with a single rimoportula in the submarginal zone of the valve face (black arrow) and one valve face fultoportula with two satellite pores near the center (arrow); scale bar = 1  $\mu\text{m}$ .

#### 3-5. *Mesodictyopsis singularis*

3, 5. External view of the valve surface with one opening of the valve face fultoportula near the center (arrow); scale bars = 1  $\mu\text{m}$ .

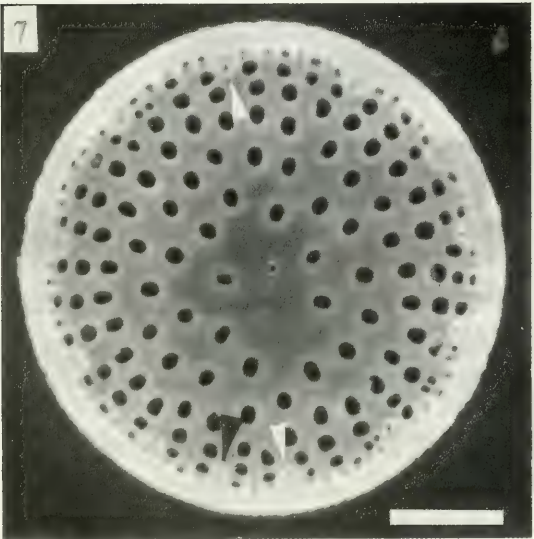
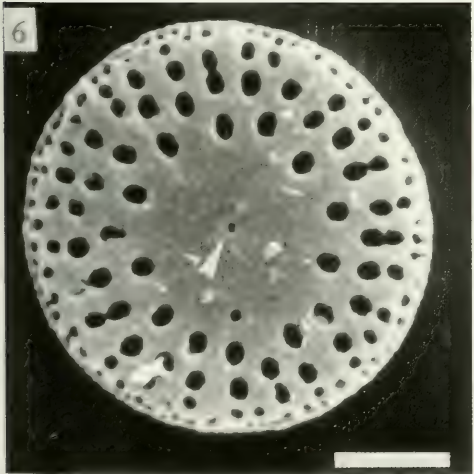
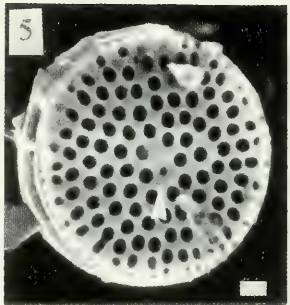
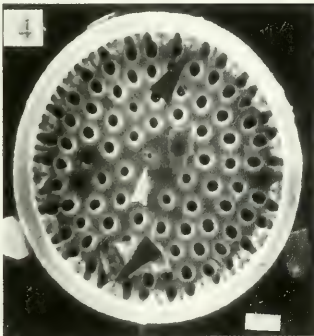
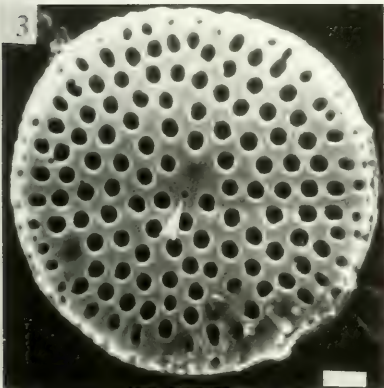
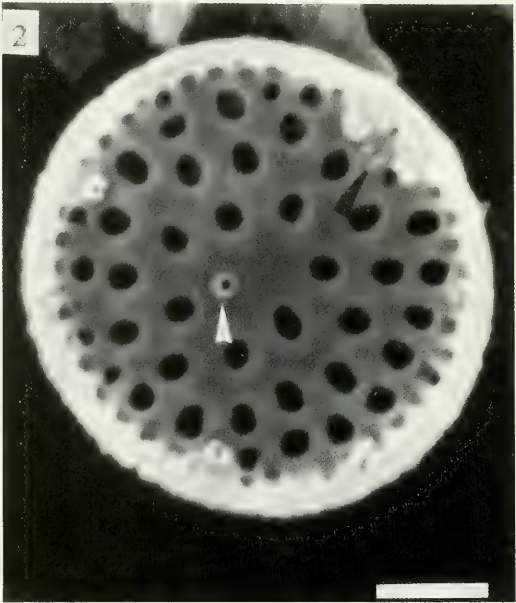
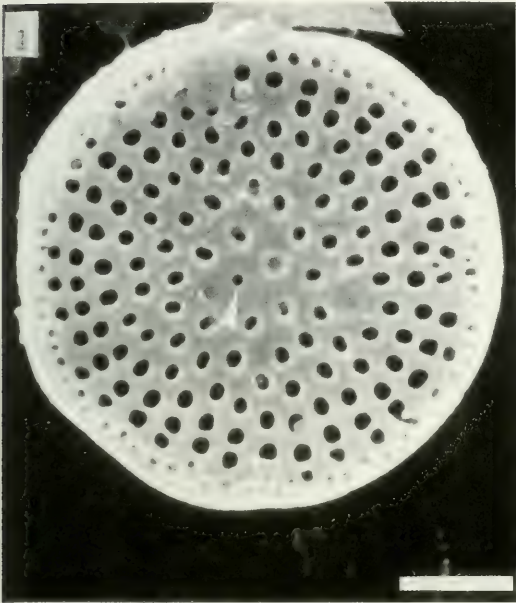
4. Internal view of the valve surface with a single valve face fultoportula with three satellite pores (arrow) and a ring of marginal fultoportulae with three satellite pores; scale bar = 1  $\mu\text{m}$ .

#### 6-7. *Mesodictyopsis similis*

6. External view of the valve surface with a wide hyaline central area and one opening of the valve face fultoportula near the center (arrow); scale bar = 2  $\mu\text{m}$ .

7. Internal view of the valve surface with a single rimoportula located on the same level with marginal fultoportulae (arrows); scale bar = 2  $\mu\text{m}$ .





## Plate 5

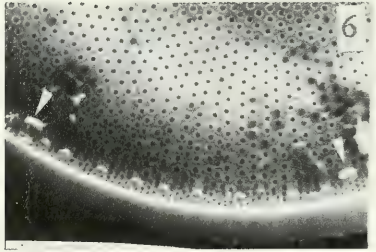
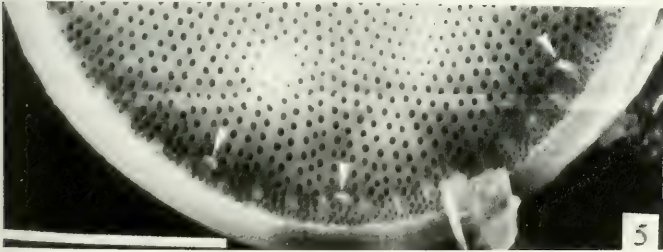
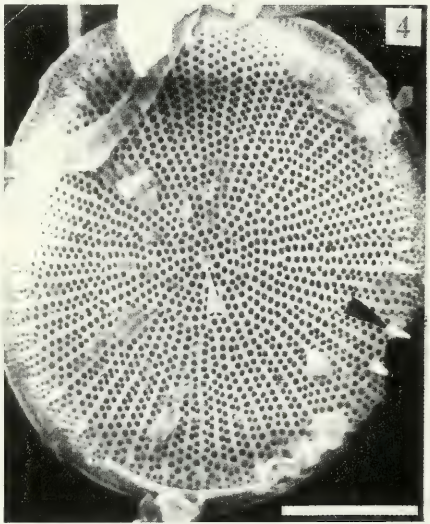
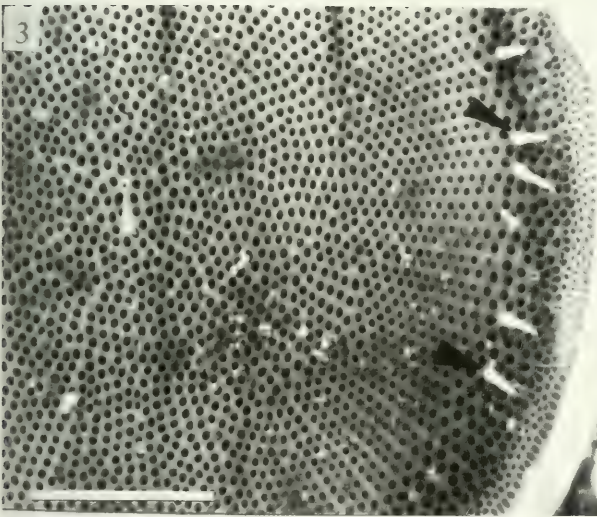
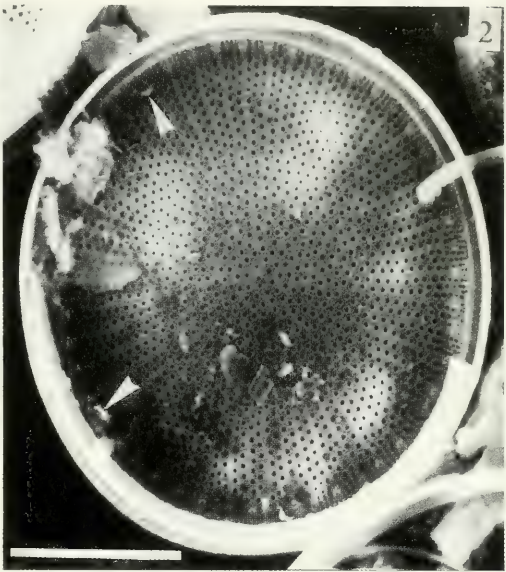
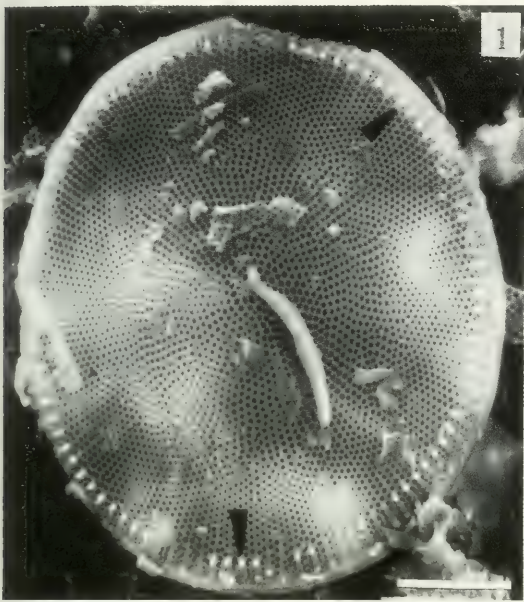
### Scanning Electron Microscopy

#### *Mesodictyopsis baicalensis*

1, 3–4. External views of the valve surface with a ring of conic spines at the valve face/mantle junction and a single opening of the valve face fulcrum portula near the center (arrows); scale bars = 10  $\mu\text{m}$  in Fig. 1, 1  $\mu\text{m}$  in Figs. 3–4

2, 5–6. Internal view of the valve surface with a marginal ring of rimoportulae (arrows); scale bar = 10  $\mu\text{m}$  Fig. 5, 1  $\mu\text{m}$  in Figs. 2, 6.







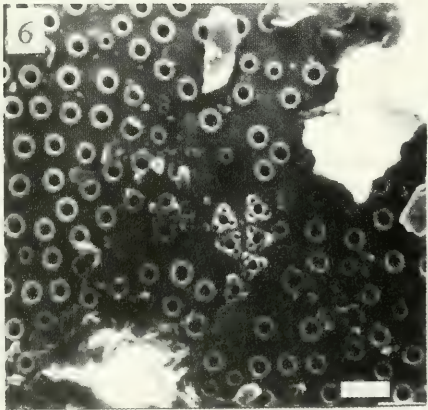
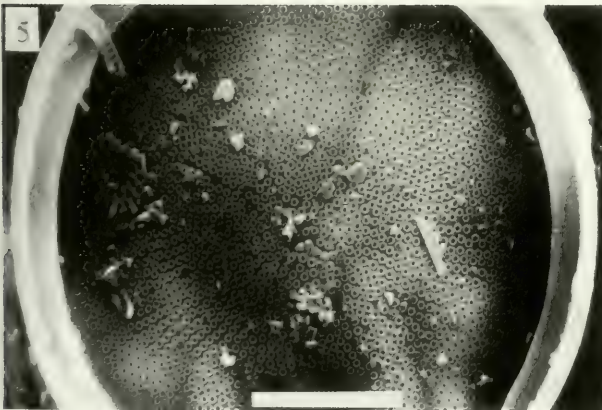
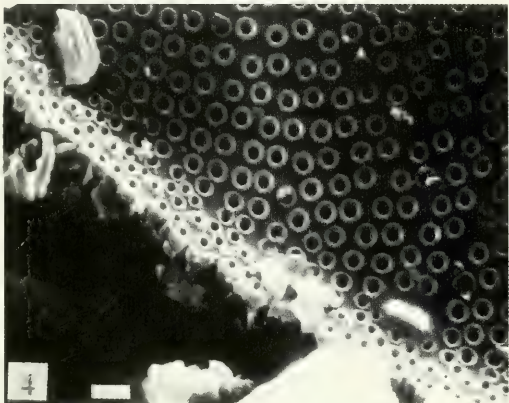
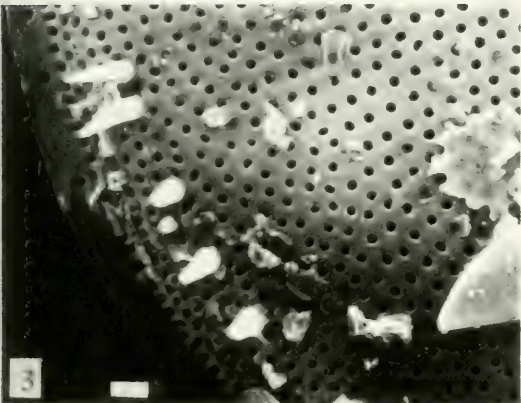
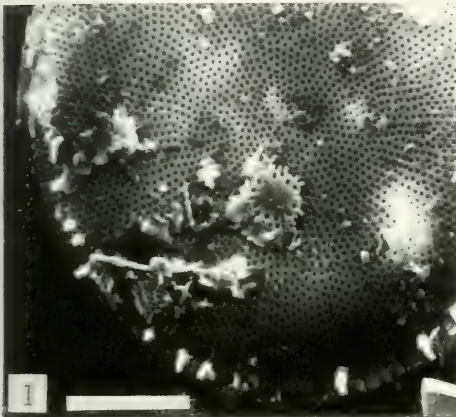
## Plate 6

### Scanning Electron Microscopy

#### *Mesodictyopsis baicalensis*

1, 3. External views showing irregularly-placed, elongate, conical spines at the valve face/mantle junction and short, thin openings of fultoportulae; scale bars = 10  $\mu\text{m}$  in Fig. 1, 1  $\mu\text{m}$  in Fig. 3.

2, 4–6. Internal valve views showing pattern of areolae, ring of many marginal fultoportulae and central fultoportulae with three satellite pores (Fig. 6); scale bars = 1  $\mu\text{m}$  in Figs. 2, 4, 6 and 10  $\mu\text{m}$  in Fig. 5.



# The Pattern of the Lateral-line System on the Caudal Fin of *Perccottus glenii* Dybowski, 1877 (Teleostei: Odontobutidae), with Comments on the Arrangement of the Lateral-line System on the Caudal Fin of Gobioidei

Harald Ahnelt and Josef Göschl

*Institute of Zoology, Department of Comparative Anatomy and Morphology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria; Email: harald.ahnelt@univie.ac.at*

The pattern of the lateral-line system on the caudal fin is surveyed in 120 genera and 200 species of gobioid fishes. In the majority of Gobioidei this sensory system is arranged in two general patterns on the caudal fin: Pattern 1 with four lateral lines, one transversal and three longitudinal, and Pattern 2 with three lateral lines, one transversal and two longitudinal. These lateral lines are formed by rows of free (superficial) neuromasts, except in the Rhyacichthyidae. In these most-basal Gobioidei, the longitudinal lateral lines are a combination of canals and free neuromasts. The transversal lateral line in Gobioidei (including Rhyacichthyidae) is always formed by free neuromasts. This transversal row is discontinuous, consisting of a few short parts (plesiomorphic), or it is continuous and relatively long (apomorphic). In some species, it is indistinct and difficult to separate from the longitudinal rows. Pattern 1 of the lateral-line system on the caudal fin is plesiomorphic for Gobioidei. As relatively rare deviations from these two patterns, an increase or a decrease in the number of longitudinal neuromast rows occurs in some Gobiidae. *Perccottus glenii* is the only known species of basal Gobioidei (including the Eleotridae) characterized by a specialized lateral-line pattern on the caudal fin. On each side of this fin, only two neuromast rows are developed: a discontinuous transversal row on its base and a long longitudinal row along its midline. This is the most specialized character state within the Odontobutidae. This research provides a further indication that the Odontobutidae are not monophyletic.

The free neuromasts of the lateral-line system of Gobioidei are arranged in series of characteristic rows and aggregations on the head, the trunk and the caudal fin. Lateral-line canals are absent on the trunk and on the caudal fin except in the Rhyacichthyidae, the most basal Gobioidei (Miller 1973; Hoese and Gill 1993). The pattern of the cephalic lateral-line system has been widely used in the classification of Gobioidei (e.g., Sanzo 1911; Iljin 1930; Miller 1986; Takagi 1988; Akihito et al. 2000; Larson 2001), but detailed information on the neuromast pattern on the trunk and on the caudal fin is rare. In most species the free neuromasts on the body are tiny and hard to detect. They are also easily damaged or abraded during collecting or preservation. This is especially true for the caudal fin. In recent years more attention has been given to the neuromast pattern on the trunk and on the caudal fin (e.g., Ahnelt and Duchkowsch 2001; Shibukawa et al. 2001; Ahnelt and Scattolin 2003).

Gobioid fishes are characterized by two general patterns of the lateral-line system of the cau-



dal fin: Pattern 1, with a transversal and three longitudinal lateral lines; Pattern 2, with a transversal and two longitudinal lateral lines (Ahnelt et al. 2000; Shibukawa et al. 2001; Ahnelt and Göschl 2003). The combination of lateral-line canals and free neuromasts is only known in the Rhyacichthyidae. In all other Gobioidae, only free neuromasts form the lateral-line system on the caudal fin. In some species, the transversal row is indistinctly developed and/or difficult to separate from the longitudinal rows. As a deviation from pattern 1, the number of longitudinal neuromast rows in some Gobiidae is increased (Mortara 1918) or decreased (Miller 1963).

Here we describe the reduced pattern of the lateral-line system on the caudal fin of the odontobutid fish *Perccottus glenii* Dybowski, 1877. Compared with the plesiomorphic arrangement of the free neuromasts on the caudal fin of the other basal Gobioidae (Rhyacichthyidae, *Terateleotris*, Odontobutidae and Eleotridae), *P. glenii* is characterized by a specialized arrangement of these neuromasts, otherwise known only in two miniature Gobiidae.

## MATERIALS AND METHODS

**NOMENCLATURE.**—**Odontobutidae:** According to Shibukawa et al. (2001) and Miller (2003), the intra-familial relationships of the Odontobutidae are unsolved and a redefinition of the Odontobutidae is needed. In the definition of the Odontobutidae, we follow, therefore, Hoese and Gill (1993) who recognize three genera within this family, *Micropercops*, *Odontobutis* and *Perccottus*. **Rhyacichthyidae:** Watson and Pöllabauer (1998) did not assign *Protogobius* Watson and Pöllabauer, 1998 to a gobioid family. In the phylogenetic tree of Akihito et al. (2000a), based on mitochondrial DNA, *Rhyacichthys* and *Protogobius* form a single cluster and were, therefore, united as Rhyacichthyidae by Shibukawa et al. (2001). In the definition of the Microdesmidae and the Ptereleotridae, we follow Thacker (2003).

Institutional abbreviations follow Leviton et al. (1985) except for: CMN(FI) = Canadian Museum of Nature; IZUW = Institute of Zoology, University of Vienna; IECB = Institute of Ecology and Conservation Biology, University of Vienna.

The following preserved specimens were examined (collection number, number of specimens, sex, SL in mm, sampling site). Length of specimens is given in standard length. The sex was determined by the shape of the urogenital papillae: longer and more pointed in males, shorter and wider in females.

## MATERIAL EXAMINED

**Odontobutidae:** *Perccottus glenii*: NMH 2003.26.1; 1 female, 76.8 mm; Hungary, Bodrog River, Satoraljaújhely. NMH 2003.27.1; 1 female, 85.3 mm; Hungary, Tisza River, Mindszent. NMH 2003.28.1; 1 male, 65.7 mm; Hungary, Bodrog River, Satoraljaújhely. NRM 23932; 2 juveniles, 25.9 – 26.8 mm; Russia, Amur River, 5 km E Troitskoye. USNM 105188; 1 male, 64.1 mm; Russia, Sakhalin Island, Khanka Lake. USNM 077008; 1 female, 91.6 mm; China, Sungari River near its junction with the Amur. IECB uncatalogued; 1 male, 101.8 mm and 1 female, 72.6 mm; Ukraine, Pond at Komarno, near River Dniestr. IECB uncatalogued; 1 male, 79.6 mm and 1 female, 104.5 mm; Ukraine, Pond at Komarno, near River Dniestr.

**Rhyacichthyidae:** *Protogobius attiti* Watson & Pöllabauer, 1998: NMW 94266, 1 male, 67.7 mm, New Caledonia, South Province, Trou Bleu River. NMW 94267, 1 female, 55.5 mm, New Caledonia, Sotuh Province, Fausse Yaté River. *Rhyacichthys aspro* (Valenciennes, 1837): CAS 138655, 1 spm., sex ?, 98.8 mm, Philippines, Mindanao, Tagaloan River. CAS 51696, 1 spm., sex?, 102.2 mm, Philippines, Luzon, Mantugil River, Villar. NMW 45968, 1 female, 97.2 mm; Indonesia, Java, Semarang. NMW 82972, 1 male, 115.2 mm; Indonesia, Moluccas. NMW 82990, 1 male?, 121.7 mm, Philippines.

## COMPARATIVE MATERIAL

Within the families, the subfamilies and the genera are listed alphabetically. The pattern of free neuromasts of the lateral-line system on the caudal fin is as follows: four rows (one transversal **lct** and three longitudinal **lcd**, **lcm** and **lcv**) (Fig. 1A–B) or three rows (one transversal **lct** and two longitudinal **lcd** and **lcm**) (Fig. 1C–D). Row **lct** is continuous at the base of the caudal fin or discontinuous, as two, three (generally), or four short rows anterior to each longitudinal row (Fig. 1). Species with two longitudinal rows are marked with an asterisk. Species with more than three longitudinal rows are marked with an §. Species with one longitudinal row (**lcm**) are marked with #. Number in parentheses is number of investigated specimens and not necessarily identical with the number of specimens in the lot.

**Odontobutidae:** *Micropercops swinhonis* (Günther, 1873), UMMZ 167389, USNM 336883 (12); *Odontobutis aurarmus*\* Vidthayanon, 1995, USNM 325486, UMMZ 223284 (6); *Odontobutis obscura*\* (Temminck & Schlegel, 1845), CAS 32827, CAS 28154, MNHN 6778, MNHN 6481, MNHN 1987-1213, USNM 264892, USNM 864893, USNM 086965, UMMZ 70284, UMMZ 142619 (25); *Odontobutis potamophila*\* (Günther, 1861), BMNH 1918.11.12.16–18 (2).

**Eleotridae: Butinae:** *Bostrychus africanus* (Steindachner, 1879), BMNH 1989.1.6: 23–29 (3); *Bostrichthys zonatus* (Weber, 1907), NMW 58166 (1); *Butis butis* (Hamilton, 1822), CAS 205539, NMW 22482 (5); *Butis koilomatodon* (Bleeker, 1849), BMNH 1988.2.8: 1–8 (4); *Kribia nana*\* (Boulenger, 1901), CAS 64486, BMNH 1918.11.12: 16–18, BMNH 1948.1.14: 291–313 (4); *Kribia kribensis*\* (Boulenger, 1907), NMW 78428 (2); *Milyeringa veritas* Whitely, 1945, BMNH 1982.2.17: 1–9 (3); *Ophiocara porocephala* (Valenciennes, 1837), BMNH 1980.10.10: 260–263 (4); *Oxyeleotris fimbriata* (Weber, 1907), BMNH 1983.8.2: 147–148 (1); *Oxyeleotris heterodon* (Weber, 1907), NMW 57206, NMW 57206 (2); *Oxyeleotris lineolatus* (Steindachner, 1867), BMNH 1983.8.2: 203–210 (4); *Oxyeleotris marmorata* (Bleeker, 1852), CAS 66251 (2); *Oxyeleotris urophthalmoides* (Bleeker, 1853), CAS 49456 (1); *Pogoneleotris microps* Weber, 1907, NMW 31456 (1); *Typhleotris pauliani* Arnoult, 1959, BMNH 1981.111.9: 19–20 (2). **Eleotrinae:** *Batanga lebretonis* (Steindachner, 1870), NMW 22275, NMW 76245, NMW 76407, NMW 58729 (11); *Bunaka gyrinoides* (Bleeker, 1853), BMNH 1983.8.2: 211–214 (3); *Dormitator latifrons* (Richardson, 1844), CAS 54392 (2); *Eleotris* sp., NMW 94987 (1); *Eleotris amblyopsis* (Cope, 1871), NMW 85500 (6); *Eleotris coxi* (Krefft, 1864), NMW 78548 (1); *Eleotris daganensis* Steindachner, 1870, NMW 22488 (1); *Eleotris fusca* (Schneider & Forster, 1801), NMW 89288 (1); *Eleotris gyrinoides* Bleeker, 1853, NMW 80754 (2); *Eleotris picta* Kner, 1863, SIO 59-358-58B (1); *Eleotris sandwicensis* Vaillant & Sauvage, 1875, NMW 78678, SIO 61-425-58A (7); *Eleotris senegalensis* (Steindachner, 1870), NMW 78553, NMW 85266 (3); *Eleotris vittata* Dumeril, 1861, BMNH 1956.9.6: 51, BMNH 1985.3.18: 191–192 (3); *Gobiomorphus basal* (Gray, 1842), BMNH 1964.12.21: 17 (1); *Gobiomorphus gobioides* (Valenciennes, 1837), NMW 22508 (1); *Gobiomorus dormitor* Lacepede, 1800, BMNH 1982.8.19: 2021–2040 (4); *Guavina guavina* (Valenciennes, 1837), NMW 14644, NMW 22531 (4); *Hypseleotris* sp., NMW 30966 (1); *Hypseleotris compressa* (Krefft, 1864), NMW 22511, NMW 22520, NMW 58165 (6); *Mogurnda mogurnda* (Richardson, 1844), BMNH 1983.8.2: 4 (2); *Mogurnda nesolepis* (Weber, 1907), NMW 22517 (1); *Mogurnda variegata* Nichols, 1951, BMNH 1983.8.2: 73–74 (2); *Ophieleotris aporos* (Bleeker, 1854), NMW 22524, NMW 22537, NMW 78607, NMW 83359 (7); *Philypnodon grandiceps* (Krefft, 1864), NMW 22534 (1).

**Gobiidae: Amblyopinae:** *Amblyopus caeculus* Karoli, 1882, NMW 5779 (2); *Taenioides buchanani* (Day, 1873), NMW 76500 (1); *Taenioides cirratus* (Blyth, 1860), NMW 94598 (1).



**Gobiinae:** *Acentrogobius caninus* (Valenciennes, 1837), NMW 28808–28811 (3); *Acentrogobius frenatus* (Günther, 1861), NMW 30452–30453 (2); *Acentrogobius masoni* (Day, 1873), NMW 33926 (1); *Acentrogobius simplex* (Sauvage, 1880), NMW 29964 (6); *Amblygobius albimaculatus* (Rüppell, 1830), NMW 28722–28727 (4); *Amblygobius byonensis* (Richardson, 1844), NMW, 33924, NMW 58800 (4); *Amblygobius sphynx* (Valenciennes, 1837), NMW 30102–30105 (3); *Amoya* sp., NMW 16165, NMW 30757 (2); *Anatirostrum profundorum*\* (Berg, 1927), CMNFI 1999–0023 (4); *Asterropteryx semipunctatus* Rüppell, 1830, NMW 22516, NMW 78225, NMW 88504 (6); *Bathygobius cotticeps* (Steindachner, 1879), NMW 30439 (1); *Bathygobius fuscus* (Rüppell, 1830), NMW 88321(5); *Bathygobius soporator* (Valenciennes, 1837), NMW 33927–33928, NMW 60391 (4); *Benthophilus stellatus*\* (Sauvage, 1874), IZUW uncatalogued (2); *Caffrogobius caffer* (Günther, 1874), NMW 28819–28820 (2); *Callogobius sclateri* (Steindachner, 1879), NMW 30901 (1); *Chasar bathybius* (Kessler 1877), CMNFI uncatalogued (4); *Chromogobius quadrivittatus* (Steindachner, 1863), NMW 30639, NMW 30657, NMW 86084, NMW 88486 (4); *Chromogobius zebratus* (Kolombatovic, 1891), NMW 29613, NMW 86082 (3); *Corcyrogobius liechtensteini* (Kolombatovic, 1891), NMW 37536–37543, NMW 78460; NMW 94458 (4); *Deltentosteus collonianus*§ (Risso, 1820), NMW 28826–28830, NMW 29087–29100, NMW 30342, NMW 86693 (6); *Deltentosteus quadrimaculatus*§ (Valenciennes, 1837), NMW 28845–28849, NMW 37479–37484, NMW 30667 (5); *Didogobius kochi* Van Tassell, 1988, IZUW uncatalogued (2); *Didogobius splechnai* Ahnelt & Patzner, 1995, NMW 92804, NMW 92805, NMW 94451 (4); *Economidichthys pygmaeus* (Holly, 1929), MCN 106376–394 (2); *Elacatinus* sp., SIO uncatalogued (1); *Elacatinus multifasciatus* (Steindachner, 1876), NMW 76239 (1); *Evermannia longipinnis* (Steindachner, 1879), NMW 76420 (2); *Eviota distigma* Jordan & Seale, 1906, NMW 88173 (4); *Favonogobius reichi* (Bleeker, 1853), NMW 33897 (1); *Gammogobius steinitzi* Bath, 1971, SMF 11071, NMW 94452–94456 (4); *Glossogobius celebius* (Valenciennes, 1837), NMW 83363 (1); *Glossogobius giuris* (Hamilton, 1822), NMW 30543–30544 (2); *Gobiodon citrinus* (Rüppell, 1838), NMW 30973 (5); *Gobiosoma bosc* (Lacépède, 1800), SIO 67-277-59 (2); *Gobius ater* Bellotti, 1888, NMW 28551–28552, NMW 29041 (2); *Gobius buccichi* Steindachner, 1870, NMW 88436, NMW 88491 (6); *Gobius cobitis* Pallas, 1814, NMW NMW 87092, NMW 88463 (6); *Gobius cruentatus* Gmelin, 1789, NMW 28986–28982 (2); *Gobius fallax* Sarato, 1889, NMW 28792, NMW 77932 (2); *Gobius gasteveni* Miller, 1974, MNCN 73576–73579, MNCN 79218–79219 (3); *Gobius geniporus* Valenciennes, 1837, NMW 87065 (1); *Gobius niger* Linnaeus, 1758, MNCN 74278–74282, IZUW uncatalogued (4); *Gobius paganellus* Linnaeus, 1758, NMW 80592, NMW 84937, NMW 94582, NMW 94583 (6); *Gobius rouli* De Buen, 1828, NMW 94277 (2); *Gobius vittatus* Vinciguerra, 1883, IZUW uncatalogued (1); *Gobiusculus flavescens*\* (Fabricius, 1779), NMW 30693 (3); *Heteroleotris vulgaris* (Klunzinger, 1871), NMW 31020, NMW 78237, NMW 88177 (12); *Istigobius diadema* (Steindachner, 1876), NMW 29171 (1); *Knipowitschia croatica*\* Mrakovic, Kerovec, Misetic & Schneider, 1996, NMW 93978 (6); *Knipowitschia caucasica*\* (Berg, 1916), LZUT uncatalogued (2); *Knipowitschia pannizae* (Verga, 1841), IZUW uncatalogued (4); *Knipowitschia punctatissima*\* (Canestrini, 1864), IZUW uncatalogued (5); *Lebetus guilleiti*# (le Danois, 1913) NMW 94589–94592 (4); *Lesueurigobius friesii* (Malm, 1874), MNCN 78580–78583; NMW 76296, NMW 88348 (4); *Lesueurigobius suerii* (Risso, 1810), NMW 88351, NMW 88550 (2); *Lophogobius cyprinoides* (Pallas, 1770), NMW 30807–30808 (2); *Lythrypnus cobalus* Bussing, 1990, CAS 205778, SIO 72-97 (2); *Lythrypnus dalli* (Gilbert, 1890), CAS 118455, SIO 63-174-59C (6); *Lythrypnus gilberti* (Heller and Snodgrass, 1903), CAS 39236 (4); *Lythrypnus pulchellus* Ginsburg, 1938, CAS 18097 (3); *Lythrypnus rhizophora* (Heller and Snodgrass, 1903), CAS 50078 (5); *Lythrypnus zebra* (Gilbert, 1990), CAS 25388, SIO H50-40-59A (6); *Mauligobius maderensis*



(Valenciennes, 1837), NMW 87554 (1); *Mesogobius batrachocephalus* (Pallas, 1814), NMW 11397 (3); *Microgobius gulosus* (Girard, 1858), NMW 87269 (3); *Millerigobius macrocephalus* (Kolombatovic, 1891), IZUW uncatalogued (2); *Myersinia filifer* (Valenciennes, 1837), NMW 86810 (1); *Neogobius cyrius* (Kessler, 1874), NMW 94327 (4); *Neogobius eurycephalus* (Kessler, 1874), NMW 92808 (2); *Neogobius fluviatilis* (Pallas, 1814), NMW 94446 (4); *Neogobius gorlap* Iljin, 1949; CMNFI 1993-0161, CMNFI 1993-0162 (3); *Neogobius gymnotrachelus* (Kessler, 1857), NMW 88596, NMW 94583 (6); *Neogobius kessleri* (Günther, 1861), IZUW uncatalogued, NMW 93977, NMW 94560 (6); *Neogobius melanostomus* (Pallas, 1814), NMW 60200 (1); *Neogobius ratan* (Nordmann, 1840), NMW 33910 (1); *Neogobius syrman* (Nordmann, 1840), CMNFI 1970-0544 (1); *Odondebuenia balearica* (Pellegrin and Fage, 1907), MNCN 107992-108042 (6); *Padogobius bonelli* (Bonaparte, 1846), IZUW uncatalogued (5); *Padogobius nigricans* (Canestrini, 1867), IZUW uncatalogued (2); *Paragobiodon echinocephalus* (Rüppel, 1830), NMW 29196 (4); *Paragobiodon modestus* (Regan, 1908), NMW 87478 (4); *Paragobiodon xanthosomus* (Bleeker, 1852), NMW 87477, NMW 87479 (2); *Pomatoschistus adriaticus*\* Miller, 1873, NMW 28647-28649, NMW 28670 (5); *Pomatoschistus kneri* (Steindachner, 1861), NMW 37772-37776 (1); *Pomatoschistus marmoratus*\* (Pallas, 1810), NMW 87359 (3); *Pomatoschistus microps* (Kroyer, 1838), IZUW uncatalogued (3); *Priolepis* sp., NMW 88507 (2); *Priolepis nuchi-fasciata* (Günther, 1873); NMW 33908 (1); *Proterorhinus marmoratus* (Pallas, 1814), NMW 60240, NMW 79755, NMW 94561, NMW 94595 (7); *Rhinogobiops nicholsii* (Bean, 1882), CAS 135015, CAS 135016, CAS 27627 (6); *Speleogobius trigloides*# Zander and Jelinek, 1976, NMW 75826-75827 (1); *Thorogobius macrolepis* (Kolombatovic, 1891), NMW 37421-37422, NMW 94331, NMW 94332 (7); *Thorogobius ephippiatus* (Lowe, 1839), NMW 86591 (1); *Trimma* sp., NMW 89332 (1); *Valenciennea sexguttat* (Valenciennes, 1837), NMW 83959 (1); *Vanneaugobius dollfusi* Brownell, 1978, NMW 87961, NMW 87962 (6); *Zebrus zebrus* (Risso, 1827), NMW 86097, NMW 88472, NMW 88492, IZUW uncatalogued (7); *Zosterisessor ophiocephalus* (Pallas, 1814), IZUW uncatalogued (1). **Gobionellinae:** *Acanthogobius flavimanus* (Temminck and Schlegel, 1845), CAS 36971, CAS 42487, CAS 52003, CAS 21367, CAS 213686, NMW 30454-30455 (28); *Aphia minuta*§ Risso, 1827, NMW 31463, NMW 88030, NHRM 46688 (10); *Arcygobius baliurus* (Valenciennes, 1837), NMW 30278-30279, NMW 82114 (4); *Awaous giuris* (Hamilton, 1822), NMW 30096 (1); *Awaous tajasica* (Lichtenstein, 1822), NMW 91265, NMW 91277 (6); *Brachygobius xanthozonus*\* (Bleeker, 1849), NMW 12685, NMW 30152-30156 (4); *Cepola striata* Bloch and Schneider, 1801, NMW 28742-28747 (3); *Clariger cosmurus*\* Jordan and Snyder, 1901, IZUW uncatalogued (2); *Chaenogobius gulosus* (Sauvage, 1882), IZUW uncatalogued, NMW 30676 (4); *Clevelandia ios*\* (Jordan and Gilbert, 1882), CAS 15476, SIO 47-73-59D (5); *Ctenogobius sagittula*\* (Günther, 1861), CAS 55185 (3); *Euclogobius newberryi*\* (Girard, 1856), CAS 31768, SIO 62-278-59A (6); *Eutaeniichthys gilli*\* Jordan and Snyder, 1901, IZUW uncatalogued (2); *Evorthodus lyricus* (Girard, 1858), NMW 83107, NMW 88633 (3); *Gillichthys mirabilis*\* Cooper, 1864), CAS 22071, CAS 79616 (6); *Gillichthys seta*\* (Ginsburg, 1938), CAS 26055, SIO 67-133-59 (6); *Gobiopterus* cf. *chuno*§ (Hamilton, 1822), IZUW uncatalogued (5); *Gymnogobius castaneus* (O'Shaughnessy, 1875), IZUW uncatalogued, NMW 78031(3); *Gymnogobius urotaenia*\* (Hilgendorf, 1879), NMW 29508 (1); *Ilypnus gilberti*\* (Eigenmann & Eigenmann, 1891), CAS 24169, CAS 26896 (6); *Ilypnus luculentus*\* (Ginsburg, 1938), CAS 214242, SIO 62-235-59A (6); *Lepidogobius lepidus*\* (Girard, 1858), CAS 19894, CAS 25383, CAS 53228 (6); *Lethops connectens*\* Hubbs, 1926, SIO H46-46, SIO H51-239 (6); *Leucopsarion petersii*§ Hilgendorf, 1880, FAKU 103091 (5); *Luciogobius guttatus*\* Gill, 1859, FAKU 102257-102258 (2); *Mugilogobius poeyi* (Steindachner, 1867), NMW 30608 (1); *Oxyurichthys papuensis* (Valenciennes, 1837), NMW 29935-29938 (3); *Oxyurichthys tentacularis*

(Valenciennes, 1837), NMW 12688 (1); *Pseudaphya ferreri*\* (de Buen and Fage, 1908) NMW 37424–37429, NMW 37431–37433 (7); *Quietula guaymasiae*\* (Jenkins & Evermann, 1889), CAS 26056, CAS 55187 (6); *Quietula y-cauda*\* (Jenkins and Evermann, 1889), CAS 11497, CAS 200221 (6); *Rhinogobius* sp\*., NMW 89618 (3); *Stigmatogobius sadanundio* (Hamilton, 1822), NMW 81598 (1); *Stigmatogobius sella* (Steindachner, 1881), NMW 30107–30108 (1); *Synechogobius ommaturus* (Richardson, 1845), NMW 34199–34200, NMW 34206–34208, NMW 81876 (4); *Triaenopogon barbatus* (Günther, 1861), CAS 161208 (2); *Tridentiger bifasciatus*\* Steindachner, 1881, CAS 82361 (3); *Tridentiger trigonocephalus*\* (Gill, 1859), CAS 15405 (1); *Typhlogobius californiensis*\* Steindachner, 1879, CAS 200223, CAS 211664 (5). **Oxudercinae:** *Apocryptes bato* (Hamilton, 1822), CAS 89289 (2); *Boleophthalmus boddarti* (Pallas, 1770), CAS 140028, IZUW 2419 (4); *Boleophthalmus pectinirostris* (Linnaeus, 1758), NMW 78444 (2); *Periophthalmus barbarus* (Linnaeus, 1766), IZUW 2418, NMW 31321 (2). **Sicydiinae:** *Sicydium* sp., NMW 31434 (1); *Sicydium plumieri* (Bloch, 1786), NMW 91574, NMW 31411–31414 (6); *Sicyopterus cynocephalus* (Valenciennes, 1837), NMW 31405–31406 (1); *Sicyopterus sarasini* Weber and Beaufort, 1915, NMW 94340 (2); *Stiphodon elegans* (Steindachner, 1879), NMW 81318 (3).

**Kraemeriidae:** *Kraemeria samoensis* Steindachner, 1906, NMW 83668 (2).

**Microdesmidae:** *Microdesmus dipus* Günther, 1864, BMNH 1967.12.30: 1–3 (1).

**Ptereleotridae:** *Nemateleotris decora* Randall and Allen, 1973, BMNH 1983.3.25: 893–895 (1); *Ptereleotris microlepis* (Bleeker, 1856), BMNH 1983.3.25: 892 (2).

## TERMINOLOGY OF THE LATERAL-LINE SYSTEM OF THE CAUDAL FIN

Sanzo (1911) was the first to develop a terminology for the longitudinal rows of neuromasts on the caudal fin of gobioid fishes. The species he investigated have three longitudinal rows of neuromasts developed on each side of the caudal fin: one an elongation of the median trunk lateral line, and ventral and dorsal to it, and two accessory rows. Sanzo named these rows ‘lateral caudal’ (**lc**) and they differed, from dorsal to ventral, between **lc**, **lc’** and **lc’’**. The number of lateral lines on the caudal fin in Gobiioidei may be secondarily reduced to one or two or increased to eight neuromast rows (Mortara 1918; Ahnelt and Göschl 2003; Scattolin and Ahnelt, unpublished), making it difficult to identify homologous rows. Therefore, an alternative classification of the lateral-line system was proposed by Ahnelt et al. (2000) and Ahnelt and Duchkowsch (2001) reflecting the position of the rows on the caudal fin: **lcd** (lateral caudal dorsal), **lcm** (lateral caudal medial) and **lcv** (lateral caudal ventral). Three longitudinal lateral lines are plesiomorphic for Gobiioidei (Springer 1983). In Gobiioidei with two longitudinal rows, the **lcd** and **lcm** are developed and the **lcv** is absent (e.g., Ahnelt et al. 2000; Ahnelt and Göschl 2003). In species with one longitudinal row (**lcm**), both accessory rows (**lcd** and **lcv**) are absent.

The characteristic pattern of the lateral-line system on the caudal fin, **lcd** separated from **lcm** by three and **lcm** from **lcv** by two fin rays, allows the identification of the three longitudinal neuromast rows in species with more than three rows developed (Fig. 1F).

The transversal row (**lct**) on the base of the caudal fin was included by Sanzo (1911) as the last transversal row in the lateral medial trunk series. These series of generally short rows run along the midline of the trunk and are associated with the trunk lateral-line canal in *Rhyacichthys*, *Protogobius* and *Terateleotris* (Wongrat and Miller 1991; Shibukawa et al. 2001). Such short transversal rows are also found on each first canal carrying scales on the caudal fin of *R. aspro*. Lateral-line canals on the trunk and on the caudal fin are absent in the other Gobiioidei. The neuromast row **lct** differs from the medial trunk series (**lm**) as it is distinctly longer, seemingly because it was orig-



inally associated with the three lateral-line canals of the caudal fin. In many advanced taxa the three parts unite to form a long, continuous transversal row, exceeding the longitudinal rows dorsally and ventrally and often nearly extending over the entire caudal fin base (Fig. 1D–F). Generally, **lct** is separated from the last **lm** row by a larger gap than the **lm** rows on the caudal peduncle from each other. The row **lct** may be reduced to three neuromasts, each anterior to one longitudinal neuromast row. In many species, these neuromasts are still identifiable due to their larger size and a gap to the neuromasts of the longitudinal rows (Fig. 1). These neuromasts of **lct** are in some taxa incorporated in the origin of the longitudinal neuromast rows and, therefore, only separable if they are of a larger size. The incorporation of **lct** in the longitudinal lateral-line rows and its secondary loss is seemingly apomorphic.

The neuromast rows on the caudal peduncle and on the caudal fin of gobioid fishes are innervated by the *ramus lateralis posterius* (Sanzo 1911; Wongrat and Miller 1991). According to the nomenclature of Coombs et al. (1988), **lct** (at the of caudal fin) is formed by secondary replacement neuromasts. Secondary replacement neuromasts, derived from free neuromasts associated with pores of the lateral-line canals (e.g., the trunk canal of *Protogobius*, *Rhyacichthys* and *Terateleotris*, and the origin of canals on the caudal fin of *Protogobius* and *Rhyacichthys*), form transverse rows along the former course of a canal. The longitudinally arranged neuromasts on the caudal fin (**lcd**, **lcm**, **lev**) form rows along the direction of deleted canals and are, therefore, primary replacement neuromasts, not secondary accessory neuromasts as postulated by Wongrat and Miller (1991).

## RESULTS

**LATERAL-LINE SYSTEM OF THE CAUDAL FIN OF *PERCCOTTUS GLENII*.**— The lateral-line system on the trunk and caudal fin is formed by free neuromasts. No trunk canal, no canal in extension of the trunk canal on the caudal fin, and no accessory canals on the trunk and on the caudal fin are developed in *P. glenii*. These canals, present in the more-basal Gobioidi *Rhyacichthys*, *Protogobius* and *Terateleotris*, are replaced by free neuromasts.

The pattern of the lateral-line system on the caudal fin is T-shaped. It consists of free neuromasts arranged in two rows on each side of the fin, one row transversal (**lct**) on the base of the fin and the second longitudinal (**lcm**) in its midline (Fig. 1E).

The transversal row is discontinuous. In adults, it extends as three distinct sections of neuromasts (short rows or accumulations) transversely between the fourth and twelfth branched caudal-fin rays. The median section extends anteriorly to the single longitudinal neuromast row. In juveniles, these three sections of the row **lct** are each represented by a single neuromast. The number of these neuromasts increases with size: in specimens > 70 mm SL, each section is represented by a short row, whereas in specimens > 100 mm SL, they are multiple rows or aggregations of neuromasts. **lct** is distinctly separated from the last row of the lateral median trunk series (**lm**) and extends over the small scales which cover the caudal fin base.

Only a single longitudinal row of neuromasts is developed, the lateral caudal median row (**lcm**). The dorsal and the ventral lateral caudal rows (**lcd** and **lev**), the first generally present in Gobioidi, the second in many species lacking, are absent. **lcm** extends along the interradiial membrane between the eighth and ninth (adult) or seventh and eighth (juveniles) branched caudal-fin rays. This row of neuromasts is long but does not reach the rear margin of the caudal fin. It extends over about three quarters of the fin in adults. The length of this row is not known for juveniles because their caudal fins were damaged in their rear parts. **lcm** begins immediately behind the last row of small scales that cover the base of the caudal fin, opposite the median section of **lct**. At the



origin of **lcm**, the neuromasts are closely set, but they are more distant from each other towards its end. In specimens >100 mm SL, this row may be doubled at its beginning.

The pattern of the lateral-line system on the caudal fin of *P. glenii* differs distinctly from the general pattern found in gobioid fishes and seemingly represents a derived condition. With only one longitudinal row of neuromasts developed, large parts of this fin are not covered by the lateral-line system. Such an arrangement of neuromasts is not known in other basal gobioid fishes including Eleotridae.

**LATERAL-LINE SYSTEM ON THE TRUNK AND THE CAUDAL FIN OF RHYACICHTHYIDAE.**—Within the Rhyacichthyidae, *sensu* Shibukawa et al. (2001), the lateral-line system of *Protogobius attiti* is obviously more specialized than those of *Rhyacichthys aspro*. Compared with the sensory system of the latter, it shows reductions in the lateral-line canals on the head and on the caudal fin (Watson and Pöllabauer 1998; Shibukawa et al. 2001). Such differences are also found in the trunk lateral-line canal.

In *R. aspro*, this canal is formed by two parts: an anterior continuous and a posterior discontinuous part. The anterior part of the trunk canal is continuous with the cephalic canal system (Akihito et al. 2000b:1272, fig. 4-1) and extends uninterrupted along about the first 12 scales of the trunk. Two canaliculi (short side branches) extend dorsally and ventrally from the canal along the posterior margin of every second lateral-line scale. Between the dorsal and ventral end of these canaliculi, the posterior margin of the scales is convex and free of ctenii. This gives the anterior lateral-line scales a characteristic shape: the center of the posterior rim of the scales is emarginated and separates the ctenii into a dorsal and ventral series. The continuous part of the trunk lateral-line canal ends with a single terminal pore. In its further course, the trunk canal is discontinuous and consists of a consecutive series of short canals, each on a single scale. The discontinuous part of the trunk canal starts somewhat dorsal to the end of the continuous trunk canal, which is bent downwards ["lateral-line interrupted at midpoint of body" of Shibukawa et al. (2001)]. These canals extend over nearly the entire surface of the lateral-line scales. Each canal ends at the posterior edge of the scale and starts below the margin of the scale in front of it. Where the canals end

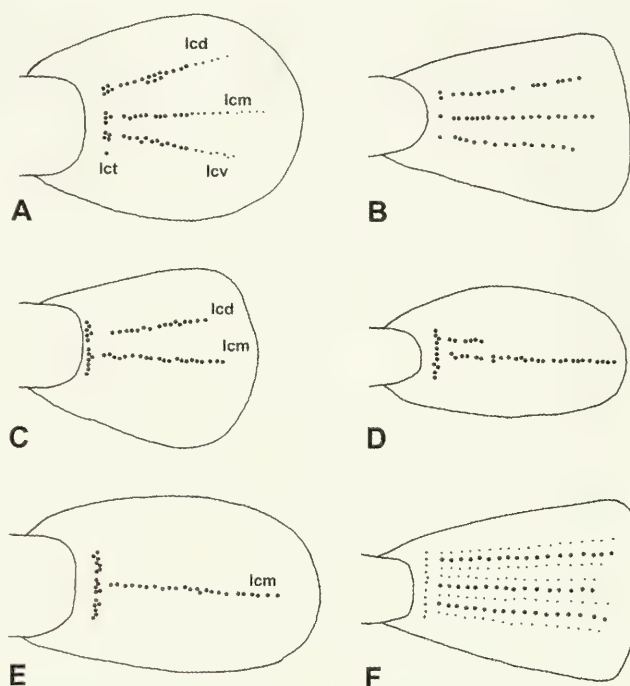


FIGURE 1. Stylized pattern of the lateral-line system on the caudal fin of Gobioidae. A–B: Three longitudinal rows of free neuromasts (A: *Gobius niger*, B: *Micropercops swinhonis*). C–D: Two longitudinal rows of free neuromasts (C: *Odontobutis aurarmus*, D: *Quietula guaymasiae*). E: One longitudinal row of free neuromasts (*Perccottus glenii*). F: Eight longitudinal rows of free neuromasts (*Aphia minuta*) (neuromasts of lcd, lcm and lcv are shown enlarged). The neuromasts are not drawn to scale, and their number is larger in each species than shown. In most Gobioidae, the neuromasts decrease in size rearwards, as shown in A only. lcd = dorsal longitudinal row, lcm = medial longitudinal row, lct = transversal row, lcv = ventral longitudinal row.

in a terminal pore, the ctenii of these scales are separated by a narrow gap and/or a "slight median notch" (Miller 1973).

A few free neuromasts accompany the anterior continuous part of the lateral-line canal (Akihito et al. 2000b:1272, fig. 4-1). Their number increases with its end. Short transversal rows of free neuromasts are associated with most canals of the discontinuous trunk canal. They run immediately before the anterior pore. Additionally, these canals are accompanied by short longitudinal rows of free neuromasts, one row dorsal and one ventral to the canal. Such longitudinal rows occur also at the end of the continuous part of the trunk lateral-line canal. Dorsal and ventral to the accessory trunk canal of *R. aspro*, which is confined to a single scale ventral to the first dorsal fin base, occur transversal accessory neuromast rows. These rows are short, do not extend onto neighbouring scales, and seemingly correspond to the anterior rows of the lateral dorsal series (**ld**) of Sanzo (1911).

Three lateral-line canals extend over about half of the caudal fin in *R. aspro*, followed by short longitudinal rows of neuromasts. These three canals (one in extension of the trunk lateral-line canal plus two accessory canals) are restricted to three single scales on the base of the caudal fin in *P. attiti*, followed by long longitudinal rows of neuromasts (Shibukawa et al. 2001; Ahnelt unpublished). [Like Shibukawa et al. (2001) these canals in the smaller of the two specimens investigated have not been found. Data of more individuals are needed for a better knowledge of the variability of this feature of *Protogobius*. Watson and Pöllabauer (1998:148) mention: "not present on *Protogobius* are two short accessory lateral lines on the caudal fin base reported in *Rhyacichthys*. . . ." Therefore, we conclude that these authors found the lateral-line canal in the midline of the caudal fin base.] In both *Protogobius* and *Rhyacichthys*, the longitudinal lateral lines on the caudal fin are asymmetrically arranged: the dorsal and the median lateral lines are separated by three caudal-fin rays, the median and the ventral lateral lines by two rays. This asymmetrical pattern is plesiomorphic for the Gobioidae.

Short transversal rows occur on the first canal carrying scales on the caudal fin of *R. aspro* immediately before the anterior pore of each lateral-line canal, together forming a transversal row (**lct**) consisting of three parts. Additionally, as single neuromasts, longitudinal neuromast rows occur on each first scale of the three lateral-line canals. We did not find neuromasts on the corresponding scales on the caudal fin of the two investigated specimens of *P. attiti*, but, possibly, they also occur in this gobioid species. Obviously, **lct** is present in the basal gobioid family, the Rhyacichthyidae, at least in the basal *Rhyacichthys*, a feature which had been overlooked by Ahnelt and Göschl (2003). The occurrence of a transversal row on the base of the caudal fin is plesiomorphic for the Gobioidae. Also plesiomorphic is an **lct** consisting of three short transversal rows. In the following, we list differences in features of the trunk and caudal fin lateral-line system between *P. attiti* and *R. aspro* not mentioned by Watson and Pöllabauer (1998) and Shibukawa et al. (2001) (features of *R. aspro* in parentheses): (i) trunk lateral-line canal not continuous with the cephalic canal system (continuous with the cephalic canal system); (ii) trunk lateral-line canal discontinuous, consisting of a consecutive series of short canals along the lateral midline except for a short part over the first two or three scales (anterior third of the trunk canal continuous); (iii) trunk canals with no side branches (= canaliculi) (continuous part of the trunk lateral-line canal with canaliculi); (iv) trunk canals on lateral-line scales short, not interrupting the continuous series of ctenii on the posterior margin of each scale (canals terminate at the posterior margin of the lateral-line scales separating the ctenii into dorsal and ventral series); (v) no longitudinal rows of accessory neuromasts dorsal and ventral to the trunk canals (short longitudinal rows of accessory neuromasts present dorsal and ventral to the canals of the discontinuous part of the trunk canal); (vi) no short transversal rows (present) on each scale of the three lateral-line canals on the caudal fin (three short

transversal rows present, together forming a discontinuous lateral caudal transversal row **lct**); (vii) no longitudinal rows of accessory neuromasts dorsal and ventral to the lateral-line canals on the caudal fin (longitudinal rows of accessory neuromasts present dorsal and ventral to the lateral-line canals on each first scale of the three lateral-line canals); (viii) no transversal accessory neuromast rows at the accessory trunk lateral-line canal (transversal accessory neuromast rows present dorsal and ventral to the accessory trunk lateral-line canal).

#### GENERAL PATTERN OF THE LATERAL-LINE SYSTEM ON THE CAUDAL FIN IN GOBIOIDEI EXCLUSIVE OF RHYACICHTHYIDAE

The following two patterns of the lateral-line system seemingly occur in the majority of gobioid fishes:

**PATTERN 1:** Plesiomorphic for Gobiioidei, exclusive of Rhyacichthyidae, are four lateral lines on the caudal fin, which are all formed by free (superficial) neuromasts. A discontinuous transversal row (**lct**) extending over the caudal fin base and three longitudinal rows: one in extension of the deleted trunk canal in the middle of the caudal fin (**lcm**) and two accessory rows, one on the dorsal part (**lcd**) and on the ventral part (**lcv**) of this fin (Fig. 1A–B). No lateral-line canals are developed. Obviously, plesiomorphic for Gobiioidei is a discontinuous **lct**, which consists of at least three short parts, each anterior to one of the three longitudinal neuromast rows. A continuous transversal row at the base of the caudal fin or its loss is seemingly apomorphic.

The three longitudinal rows are generally long and extend onto the interradi al membranes between two branched caudal-fin rays in the same asymmetrical pattern as in the Rhyacichthyidae. Typically, the gap between **lcd** and **lcm** is larger than the gap between **lcv** and **lcm**. Generally, these neuromast rows do not run in the midline between two fin rays: **lcd** and **lcm** follow the ventral side of a fin ray, **lcv** follows the dorsal side of a fin ray. This pattern of the longitudinal lateral lines on the caudal fin seemingly is shared by the majority of Gobiioidei. In species with rounded or pointed caudal fins, **lcm** generally is the longest row, and the two accessory rows (**lcd**, **lcv**) are more or less of similar length.

**PATTERN 2:** This pattern is derived from Pattern 1 and formed by three neuromast rows with one longitudinal row (**lcv**) lost: one transversal and two longitudinal rows (Fig. 1C). The transversal row is often continuous and in its length not affected by the loss of **lcv**. It still extends onto the ventral part of the caudal fin base. As in species with three longitudinal lateral lines, **lcd** and **lcm** are separated by three fin rays. Generally, **lcm** is somewhat longer than **lcd** (rounded caudal fin) or distinctly longer (pointed caudal fin). In several species with a rounded caudal fin, a seemingly derived condition occurs with **lcm** shortened and **lcd** the longest row. A deviation of Pattern 2 towards a pattern with only one longitudinal row occurs in the California bay gobies of the *Chasmichthys* group, *sensu* Birdsong et al. (1988). In some species, **lct** is shortened to only a few neuromasts (Ahnelt and Göschl 2003; Ahnelt unpublished) (Fig. 1D).

**DEVIATIONS FROM THE GENERAL PATTERN.**— We found three distinct deviations from the two general patterns of the lateral-line system on the caudal fin. These deviations occur in the group of Gobiioidei exclusive of the Rhyacichthyidae, the unassigned *Terateleotris*, and the Eleotridae, but including the Odontobutidae. All investigated species of the Rhyacichthyidae and Eleotridae (and *Terateleotris*) are characterized by three lateral lines on the caudal fin except for two eleotrine species, *Kribia nana* and *K. kribensis*.

(i) Longitudinal neuromast rows on the caudal fin arranged symmetrically:

This is a deviation from Pattern 1 with the three longitudinal lateral lines arranged asymmetrically. In this deviation both accessory neuromast rows (**lcd**, **lcv**) are separated from **lcm** by three



fin rays. Such a pattern occurs in two species, *Synechogobius ommaturus* and *Acanthogobius flavimanus*. Seemingly, the symmetric arrangement of the neuromasts is a derived character that developed from a pattern with **lev** separated from **lcm** by two fin rays. An indication for this hypothesis is the occurrence of a second **lev** between the second and third fin ray below **lcm** in *A. flavimanus*. Such doubled **lev** occurs in 46% of the investigated specimens, but only in 10% on both sides of the fin. Except for one specimen with a second **led**, this row and **lcm** were never doubled. Possibly because of the low number of specimens investigated, no fourth row has been found in *S. ommaturus*. The question of whether three longitudinal rows arranged symmetrically on the caudal fin are a characteristic feature for the *Acanthogobius*-group, *sensu* Pezold (1993), is currently under investigation by the senior author.

(ii) Longitudinal neuromast rows decreased in number, loss of **led** and **lev**:

This deviation, only a single longitudinal neuromast row (**lcm**) developed, obviously occurs independently twice within the Gobioidae: in the Odontobutidae, and in the derived Gobiidae.

*Perccottus glenii* is the only known representative of an assemblage of basal Gobioidae (Rhyacichthyidae, Odontobutidae and Eleotridae) with a single neuromast row on the caudal fin. The pattern of the lateral-line system of this species is described above. It is not known whether this arrangement derived from a pattern with two or with three longitudinal neuromast rows.

Two species of Gobiidae, *Lebetus guilleti* and *Speleogobius trigloides*, are also peculiar with only one longitudinal row (**lcm**) on the caudal fin developed (but concluding from Miller (1963), *L. guilleti* can also have two longitudinal rows developed). The arrangement of the lateral-line system on this fin is very similar for both species and represents a derived condition, a further indication of a close relationship as recently proposed by Herler and Kovacic (2002). *L. guilleti* and *S. trigloides* are tiny gobies of about 20 mm SL generally characterized by a reduced neuromast pattern on the body like, as known for many small gobies (Ahnelt and Bohacek 2004, and authors summarized therein). Some neuromast rows on the head are completely absent and many reduced to one or only a few neuromasts (Miller 1963; Zander and Jelinek 1976). The loss of two longitudinal rows on the caudal fin is seemingly not necessarily the result of miniaturization. Other tiny gobies, such as *Corcyrogobius liechtensteini* (the smallest Mediterranean gobiid fish) and *Gobiopterus chuno*, have three or more longitudinal rows on this fin developed.

(iii) Longitudinal rows increased in number:

Sporadically, gobioids can be found with a supernumerary longitudinal neuromast row on the caudal fin. These specimens display four longitudinal rows but, generally, only on one side of the fin (Ahnelt unpublished). Such supernumerary rows occur rarely and are not typical for the species.

Gobioids with distinctly more than three longitudinal neuromast rows have these rows generally separated by one fin ray only (Mortara 1918; Scattolin and Ahnelt, unpublished). This highly specialized pattern is so far only known within the Gobiidae and seemingly evolved independently several times within this gobioid family.

Three species are known with eight rows of neuromasts on the caudal fin: the north-eastern Atlantic species *Aphia minuta*, and the Pacific gobies *Gobiopterus chuno* and *Leucopsarion petersii*. In these species, **lct** is continuous and long, extending nearly over the entire caudal fin (Fig. 1F). The eight longitudinal rows extend onto the interradiial membranes between the second and the tenth segmented and branched fin rays, each separated from the other by one fin ray. These three species can be considered as derived forms and are characterized by paedomorphic features such as completely absent head canals, transparent bodies and pelagic life style. For these evolved pelagic Gobiidae, a convergent evolution of free neuromast pattern on the caudal fin in adaptation to similar habitats is assumed (Scattolin and Ahnelt, unpublished).

Two Atlantic-Mediterranean species of the genus *Deltentosteus* also have an increased num-

ber of neuromast rows on the caudal fin, but with four (*D. quadrimaculatus*) and six (*D. colloni-  
amus*) rows distinctly less than the above-mentioned species. A detailed description of the neuro-  
mast pattern on the caudal fin of these two species and a discussion if the increase in neuromast  
rows possibly following a certain order are under study by the senior author.

## DISCUSSION

Three longitudinal lateral lines on each side of the caudal fin are characteristic for the basal  
gobioid genera *Rhyacichthys* Boulenger, 1901, *Protogobius* Watson and Pöllabauer, 1998 and  
*Terateleotris* Shibukawa et al., 2001 (Springer 1983; Shibukawa et al. 2001). This pattern is also  
known from basal Perciformes (Jakubowski 1966, 1967). In all Gobioidae except the Rhyac-  
ichthyidae, *sensu* Shibukawa et al. (2001), these lateral lines are formed only by free neuromasts.  
Further, a discontinuous transversal lateral line on the base of the caudal fin formed by three short  
sections and plesiomorphic for Gobioidae is a feature seemingly also occurring in basal Perci-  
formes (Jakubowski 1966, 1967).

Three or two longitudinal rows of neuromasts occur on the caudal fin of most Gobioidae with  
a fourth or third, transversal row more or less distinctly developed on the fin base (Sanzo 1911;  
Miller and El-Talwil 1974; Ahnelt and Duchkowitsch 2001; Shibukawa et al. 2001) (Fig. 1A–B).  
In species with two longitudinal rows on the caudal fin, the ventral row **lev** is absent (Ahnelt et al.  
2000; Ahnelt and Göschl 2003), a feature that occurs in the Odontobutidae, Eleotridae (Eleotrinae)  
and Gobiidae (Gobiinae and Gobionellinae) (Fig. 1C–D). [From a figure of a generalized sicydiine  
gobiid shown by Parenti and Maciolek (1993, fig. 3), Ahnelt and Göschl (2003) concluded that  
Sicydiinae have only two longitudinal rows of neuromasts on the caudal fin. However, all species  
investigated for this study have three longitudinal rows with the neuromasts invaginated and diffi-  
cult to detect].

Three longitudinal neuromast rows occur in the Rhyacichthyidae (preceded by lateral-line  
canals), *Terateleotris* (unassigned genus), Odontobutidae, Eleotridae, Gobiidae (Amblyopinae,  
Gobiinae, Gobionellinae, Oxudercinae, Sicydiinae), Kraemeriidae, Microdesmidae and Ptereleotr-  
idae. Each of these longitudinal neuromast rows extends onto the interradi-  
al membrane between two branched caudal-fin rays in a characteristic pattern. Typically for Gobioidae with three longi-  
tudinal lateral lines is a larger distance between **lcd** and **lcm** than between **lev** and **lcm** (Fig. 1A–B).  
This is the case because **lcd** is separated from **lcm** by three fin rays and **lcm** from **lev** by two fin  
rays. In species with two longitudinal lateral lines (**lcd** and **lcm**), these are also separated by three  
fin rays. Additionally, the neuromast rows do not run in the midline between two fin rays: **lcd** and  
**lcm** follow the ventral side of a fin ray, **lev** follows the dorsal side of a fin ray. Seemingly, this pat-  
tern of the longitudinal lateral lines on the caudal fin is shared by most gobioids.

A transversal row (**lct**) at the base of the caudal fin seems to be developed regularly and has  
been found in all above-mentioned families and subfamilies of Gobioidae including the  
Kraemeriidae, Microdesmidae and Ptereleotridae (Fig. 1). In Gobiinae, **lct** often consists of only a  
few neuromasts, and in some species it is difficult to distinguish from the longitudinal rows. In gob-  
iine species this row consists often only of a single neuromast immediately anterior to each of the  
three longitudinal rows. Often these three neuromasts are somewhat larger than those of the longi-  
tudinal rows and separated from them by a more or less distinct gap. Additionally, a single neuro-  
mast or a short neuromast row below the origin of the most ventral longitudinal row (generally **lev**)  
forms the ventral end of **lct** (Fig. 1A). Nevertheless, in such species the pattern of the transversal-  
ly arranged neuromasts follows the asymmetric pattern of the longitudinal neuromasts. A deviation  
from this arrangement occurs in *L. guillei*. In this species, three neuromasts are arranged transver-



sally (**let**) at the base of the caudal fin, distinctly separated from the single longitudinal row (**lcm**). The dorsal neuromast of **let** is separated from the medial neuromast by only two caudal-fin rays, and the ventral neuromast by only one ray. This peculiar pattern is possibly the result of a reduced number of caudal-fin rays and a specialization. The caudal-fin rays of the related and similar tiny *S. trigloides* are more numerous, and the three neuromasts of **let** are separated from each other in the characteristic pattern described above.

A transversal neuromast row occurs independently in Gobiioidei, generally at the base of the caudal fin if two or three longitudinal rows are present (Ahnelt and Scattolin 2003; Ahnelt and Bohacek 2004); it also occurs in the basal Gobiioidei Rhyacichthyidae and in *Terateleotris*. *T. aspro* belongs to an assemblage of basal Gobiioidei with a trunk lateral-line canal developed, but is derived in the absence of lateral-line canals on the caudal fin. The pattern with four neuromast rows on this fin (one transversal and three longitudinal rows) is plesiomorphic for all Gobiioidei with lateral lines consisting only of free neuromasts. The transversal row (**let**) on the caudal fin base of *T. aspro*, figured by Shibukawa et al. (2001:fig. 6A), is discontinuous, similar to that of the Rhyacichthyidae. A discontinuous **let**, consisting of three parts, is likely plesiomorphic for the Gobiioidei.

The Odontobutidae are treated by most authors as the sister group of all other non-rhyacichthyid Gobiioidei (e. g., Hoese and Gill 1993; Akihito et al. 2000; Shibukawa et al. 2001; Wang et al. 2001; Thacker 2003). It is, therefore, interesting that in the five species we investigated (*Micropercops swinhonis*, *Odontobutis aurarmus*, *O. obscura*, *O. potamophila* and *Perccottus glenii*) the lateral-line system on the caudal fin is developed in three different patterns: (i) *M. swinhonis*, with three longitudinal rows (**lcd**, **lcm**, **lev**) and a transversal row (**let**) reduced to three (sometimes four) neuromasts each close to the origin of the longitudinal rows (Fig. 1B), (ii) *O. aurarmus* and *O. obscura* with two longitudinal rows (**lcd**, **lcm**) and a transversal row (Fig. 1C), and (iii) *Perccottus glenii* with one longitudinal row (**lcm**) and a transversal row (Fig. 1E) [Wongrat and Miller (1991) and Miller (2003) mention three longitudinal rows on the caudal fin of *P. glenii*]. All five odontobutid species are peculiar in having a derived pattern of free neuromasts on the caudal fin, with *P. glenii* having the most specialized one.

The intra-familial relationships of the Odontobutidae (*sensu* Hoese and Gill 1993) are unresolved (Akihito et al. 2000; Shibukawa et al. 2001; Thacker 2002). The arrangement of the lateral-line system on the caudal fin is possibly a further indication that the Odontobutidae are not monophyletic. The presence of three longitudinal lateral lines in *M. swinhonis* is plesiomorphic, but a transversal neuromast row reduced to three single neuromasts is apomorphic for Gobiioidei. Two longitudinal lateral lines in *O. aurarmus* and *O. obscura* and one in *P. glenii* are also derived characters. This neuromast pattern on the caudal fin of *P. glenii* is the most specialized within the Odontobutidae.

The pattern of the lateral-line system on the caudal fin of odontobutid species is obviously more diverse than those of other gobioid species. In the group consisting of all gobioids except the Odontobutidae and Rhyacichthyidae, the Eleotridae are seemingly conservative in this character. We investigated species of 20 of the 34 or 35 eleotrid genera (Thacker 2003). All, except for one genus (*Kribia*), have the plesiomorphic three longitudinal neuromast rows developed.

The lateral-line system on the trunk and caudal fin is less variable than on the head of Gobiioidei. This explains why the lateral-line system of the head is widely used as an important taxonomic tool for the classification of gobioid fishes. On the other hand, the more conservative character of the neuromast pattern on the caudal fin allows us to hypothesize that the group of gobioids classified as Odontobutidae (*sensu* Hoese and Gill 1993) appeared early in the evolution of the Gobiioidei and possibly evolved from a sister group within the Eleotridae. This hypothesis is supported by a series of plesiomorphic features that place the Odontobutidae closer to the origin of the



Gobioidei than to the Eleotridae (Hoese and Gill 1993). The Eleotridae have a more conservative pattern of neuromasts on the caudal fin as the investigated odontobutid taxa of *Micropercops*, *Odontobutis* and *Perccottus*.

Finally, it can be concluded from the above results that the decrease and the increase of the number of longitudinal neuromast rows on the caudal fin in Gobioidei follow a certain order. A reduction in the number of neuromast rows obviously first affects the ventral row (**lv**) (Fig. 1A – E). By far, the majority of Gobioidei has three or two longitudinal rows developed on the caudal fin. Only a few species are known with the number of longitudinal rows increased or further decreased. Obviously, the dorsal row (**ld**) is the next affected by reduction. In many species with only two longitudinal rows developed, this dorsal row is as a first step often distinctly shortened (e.g., Ahnelt and Göschl 2003) (Fig. 1D). In species with a single longitudinal row, the median row (**lm**) is always present (Fig. 1E).

As with a decrease in neuromast rows, so too an increase of longitudinal neuromast rows on the caudal fin follows a scheme, a phenomenon currently under study by the senior author. In the first step (four longitudinal rows), the additional row is added ventrally, and with the addition of more rows, the gaps between **lv**, **lm** and **ld** are closed. Finally, all longitudinal neuromast rows are separated by only a single fin ray.

#### ACKNOWLEDGMENTS

We thank D.J. Siebert, O.A. Crimmen (BMNH), W.N. Eschmeyer, T. Iwamoto, D. Catania (CAS), E. Miksch, H. Wellendorf (NMW), P.A. Hastings, R.H. Rosenblatt, C. Klepadlo, H.J. Walker (SIO) for their support and hospitality during our visits and for the loan of material. We also thank B.W. Coad, S. Laframboise (CMN), I. Nakamura, S. Harada (FAKU), F. Schiemer (IECB), J. Dorda-Dorda, A. Garvia (MNCN), P. Pruvost (MNH), A. Sevcic (NMH), S.O. Kullander, E. Ahlander (NRM), G.R. Smith, D.W. Nelson (UMMZ) and R.P. Vari, S.L. Jewett (USNM), for making material available.

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## ***Gorgasia thamani*, a New Species of Garden Eel from Fiji (Teleostei: Congridae: Heterocongrinae)**

David W. Greenfield<sup>1,3</sup> and Sean Niesz<sup>2</sup>

<sup>1</sup> California Academy of Sciences, 875 Howard Street, San Francisco, California 94103;

<sup>2</sup> Department of Zoology, University of Hawaii, Honolulu, Hawaii 96822.

A very elongate garden eel, *Gorgasia thamani*, is described from Koro Island, Fiji. The new species is most similar to *G. barnesi*, known from the Philippines, Papua New Guinea, and the Solomon Islands, but differs by being more slender with a shorter head and mouth and a different head pore pattern.

While conducting a survey of the marine fishes of Fiji, a colony of very elongate garden eels was discovered at the west side of Koro Island, Fiji, off Kade Village on a fine sand bottom in 14 to 15.2 m of water. The species, although similar in appearance and length to *G. barnesi*, differs from that species in a number of characters and is described here. *Gorgasia barnesi* is known from Indonesia, the Philippines, Papua New Guinea, and the Solomon Islands.

The new species is placed in the genus *Gorgasia* because the upper lip is not confluent medially across the face of the snout, the anterior nostrils and ethmoid sensory pores are separate from the upper lip, and the mouth is relatively large and slightly oblique, its angle reaching to below anterior half of eye, characters not present in the only other genus in the subfamily, *Heteroconger*.

### MATERIALS AND METHODS

Information for the holotype is presented first, followed by the range and mean or mode for all type material. All measurements are presented first as thousandths of total length, and then again as either percentage of snout-anus length or percentage of head length for comparison with data presented in Castle and Randall (1999). Methods of counting and measuring follow Castle and Randall (1999), who followed Böhlke (1989), Smith (1989) and McCosker et al. (1989). Institutional abbreviations are as listed in Leviton et al. (1985).

### SPECIES DESCRIPTION

***Gorgasia thamani* Greenfield and Niesz, sp. nov.**

(Figs. 1–5)

**MATERIAL EXAMINED.**— HOLOTYPE: CAS 219365, 1101.4 mm TL, Fiji, Koro Island, west side off Kade Village, 17°21.261'S, 179°22.435'E, sand, 14–15.2 m, 10 November 2002, field number G02-164, collected by D.W. Greenfield, K.R. Longenecker, K.S. Cole and R.C. Langston. PARATYPES: all collected with holotype: BPBM 39441, 1186 mm TL; FMNH 113585, 1180 mm TL;

<sup>3</sup> Research Associate, Department of Ichthyology, California Academy of Sciences and Emeritus Professor, University of Hawaii. Mailing address: Moss Landing Marine Laboratory, 8272 Moss Landing Road, Moss Landing, CA 95039.



USNM 376279, 1185 mm TL; BM(NH) 2004.4.8.1, 1053 mm TL; AMS I.43260-001, 913 mm TL; NSMT-P68327, 831 mm TL; SAIAB 74101, 776 mm TL; CAS 219366 (2), 705–752 mm TL.

OTHER MATERIAL COLLECTED WITH THE TYPE SERIES — CAS 219367 (29), 680–1141 mm TL.

ADDITIONAL MATERIAL EXAMINED — *Gorgasia barnesi*: Indonesia, Ambon: BPBM 36482(7) 422–1209 mm TL.

**DIAGNOSIS.**— An elongate, slender species of *Gorgasia* (depth at gills 0.69–0.91 percent total length) having 41–44 preanal pores, 69–75 preanal vertebrae, 213–225 total vertebrae, head pores POM 6+2 and ST 1+2, head 9.2–10.9 percent of snout-anus length, and mouth length 2.7–3.2 percent of snout-anus length.

**DESCRIPTION.**— Vertebral formula 7/69/213, 6–8 (usually 7), 69–75, 213–225. Lateral-line pores before anus 41, 41–44 (usually 42–44). Total lateral-line pores 120, 118–123 (usually 122). Pectoral-fin rays 13, 11–13 (usually 11). Dorsal rays before anus 167 (holotype only). Total dorsal-fin rays 571 and total anal-fin rays 381 in holotype. Head pores in holotype SO 1 + 4, IO 2 + 4, POM 6 + 2, ST 1 + 2. Proportions as thousandths of total length: snout-anus length 262.2 (262.2–318.0; 295.1); head length 28 (26.6–34.6; 29.3); snout length 5.3 (4.8–6.3; 5.3); eye diameter 5.2 (4.5–7.9; 5.7); gill opening 2.7 (2.5–3.3; 2.9); pectoral-fin length 4.1 (3.9–6.0; 4.6); depth at gill opening 7.2 (6.9–9.1; 7.9); depth at anus 4.8 (4.8–8.8; 6.8); front of upper jaw to rictus 8.4 (7.7–9.9; 8.8); front of upper jaw to end of maxilla 10.3 (9.5–14.7; 10.7). Proportions as percent of snout-anus length: head length 10.7 (9.2–10.9; 9.9); predorsal length 11.7 (9.1–11.7; 10.6). Proportions as percent of head length: snout length 18.9 (17.5–20.3; 18.6); eye diameter 18.6 (17.0–23.0; 19.8); front of upper jaw to rictus 3.2 (2.7–3.2; 3.0); gill opening 9.7 (9.0–11.8; 9.9); pectoral-fin length 14.7 (12.6–18.7; 16.0); depth at gills 25.6 (25.2–31.9; 27.4); depth at anus 17.0 (17.0–28.8; 23.4).

Color of fresh specimen: Background coloration gray, paler anteriorly and ventrally on head.

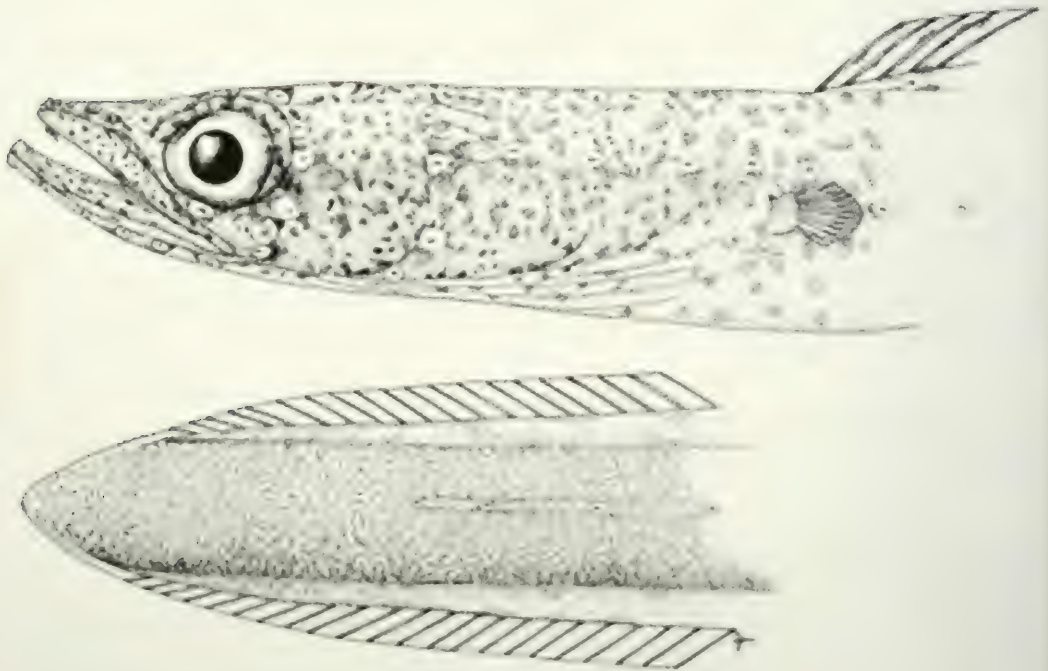


FIGURE 1. Holotype of *Gorgasia thamani*, CAS 219365.

Body covered with dense, irregular, brown spots; tip of tail and snout almost solid brown. Brown spots less dense ventrally on head and on pectoral fins. Pores on head and anterior portion of lateral line within distinct white spots. Pupil black; iris light yellow.

Color in alcohol: Background coloration mottled brown-gray; body covered with dense, irregular brown spots. Tip of tail light brown. Jaws and underside of head cream with scattered brown spots. Pores on head and anterior portion of lateral line within distinct white spots. Pupil of eye white; iris black.

**ETYMOLOGY.**— Named in honor of Dr. Randolph R. Thaman, Professor of Pacific Islands Biogeography at the University of the South Pacific in Fiji, who has provided unending assistance to us in arranging for the Survey of Marine Fishes Project funded by the National Science Foundation. Without Dr. Thaman’s assistance this project literally would not have been possible. In addition, Dr. Thaman is a leader in promoting conservation measures in Fiji, both terrestrial and marine.

**COMPARISONS.**— *Gorgasia thamani* is most similar to *G. barnesi* Robinson and Lancraft, and keys to that species using Castle and Randall (1999) because of its high total vertebral and lateral-line pore counts and coloration. It also is a large species, our largest specimen is 1185.8 mm, whereas the largest specimen of *G. barnesi* examined by Castle and Randall (1999) was 1212 mm, the largest known for a garden eel. It differs from *G. barnesi*, however, by being a more slender, elongate species, with the depth at the gills 0.69–0.91 percent of total length versus 1.1–1.6 in *G. barnesi* (Fig. 3). It also has a shorter head length, 9.2–10.9 versus 11.2–14.1 percent of snout-anus length (Fig. 4). The mouth, as measured by front of upper jaw to rictus, is shorter in *G. thamani*, 2.7–3.2 percent of snout-anus length, versus greater than 3.6 in *G. barnesi* (Fig. 5). Head pores are POM 6+2 and ST 1+2 in *G. thamani* versus POM 5+4 and ST 2+1 in *G. barnesi*.

ACKNOWLEDGMENTS

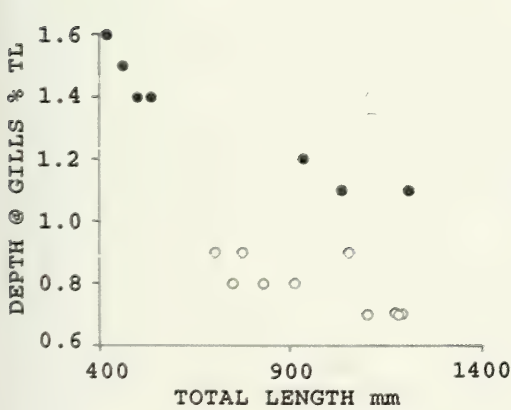


FIGURE 3. Body depth at gills as percentage of total length, open circles = *Gorgasia thamani*, closed circles = *Gorgasia barnesi*.



FIGURE 2. Dentition of holotype of *Gorgasia thamani*, upper jaw on left.

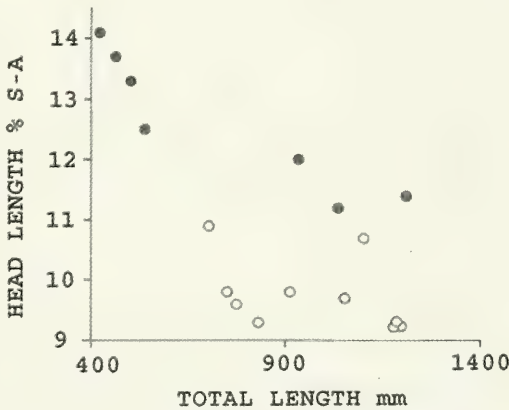


FIGURE 4. Head length as percentage of snout-anus length, open circles = *Gorgasia thamani*, closed circles = *Gorgasia barnesi*.

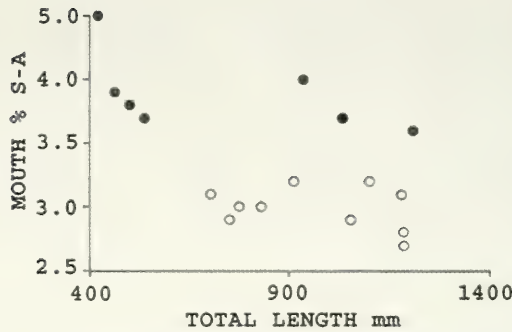


FIGURE 5. Mouth length as percentage of snout-anus length, open circles = *Gorgasia thamani*, closed circles = *Gorgasia barnesi*.

We would like to thank K.R. Longenecker, K.S. Cole, and R.C. Langston for assistance in collecting specimens, and Captain B. Vasconcellos and the crew of the *Moku Moku Hine* for assistance in the field. We are grateful to J. Seeto, G.R. South, R.R. Thaman, and R.W. Tuxton of the University of the South Pacific, Fiji for facilitating our collecting in Fiji. We also thank the Fijian Government and local village chiefs for permission to collect fishes. Special thanks are due Susan Monden for drawing the figures. This research was supported by National Science Foundation grants INT97-29666 and DEB0-1027545, and Sea Grant Project R/FM-6PD.

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# Notes on *Drypta longicollis* MacLeay and the Status of the Genus-group Name *Desera* Dejean, 1825 (Coleoptera: Carabidae: Dryptini)

Hongbin Liang<sup>1</sup>, David H. Kavanaugh<sup>2</sup>, and Mingyi Tian<sup>3</sup>

<sup>1</sup> Institute of Zoology, Beijing 100080, China; <sup>2</sup> California Academy of Sciences, 875 Howard Street, San Francisco, California 94103, USA; <sup>3</sup> South China Agricultural University, Guangzhou 51064, China

The taxonomic status of *Drypta longicollis* MacLeay, 1825, mistreated as *Desera longicollis* (MacLeay) for over a century, is clarified as a species of *Drypta* Latreille. With *Drypta longicollis* as type species, genus *Desera* Dejean is a subjective junior synonym of *Drypta*; and *Dendrocellus* Schmidt-Göbel is the valid generic name for species with pectinate tarsal claws previously included in *Desera*. Specimens identified as *Drypta longicollis* MacLeay in Andrewes' collection (The Natural History Museum, London) are found instead to represent *Dendrocellus unidentatus* (MacLeay, 1825). Enhanced descriptions of *Drypta longicollis* and *Dendrocellus unidentatus* and photographs of their type specimens are provided.

*Desera* Dejean (1825) is one of the two Old World genera currently recognized in tribe Dryptini of family Carabidae. Its members differ from those of the other genus, *Drypta* Latreille (1796), in having pectinate tarsal claw (Andrewes 1936). To date, 18 *Desera* species have been described (Lorenz 1998a), mainly distributed in southeastern Asia.

While sorting specimens of Carabidae in the collection of the Institute of Zoology (IOZ), Beijing, the first author (Liang) discovered several interesting *Desera* specimens collected from Yunnan Province, China. These specimens with brown femora, black tibia, and acute outer angles of their elytra keyed out as *Desera longicollis* (MacLeay 1825), based on the works of Heller (1923:303), Andrewes (1936:136) and Hansen (1976:403). However, Jedlička's monograph (1963:486) indicated that, in *D. longicollis* (MacLeay), the "Aussenwinkel der Flügeldecken stumpf" [outer angles of elytra acute]. In an effort to resolve this contradiction, Liang wrote to Dr. Thierry Deuve at the Muséum National d'Histoire Naturelle (MNHN) in Paris to request information about the type specimens of this species. Deuve kindly examined the types and informed Liang that the outer angle of each elytron in the types of *Drypta longicollis* MacLeay were rounded (Fig. 1), not acute.

Liang then sent his specimens to the third author (Tian) in MNHN for comparison. Subsequent morphological comparison revealed that these specimens were not identical to those of *D. longicollis*. Tian also noticed that the types of *Drypta longicollis*, with simple claws, were actually members of the genus *Drypta*, the genus in which this species was originally described, and not of the genus *Desera* as presently conceived. Subsequently, Liang borrowed specimens of *Desera unidentata* (MacLeay 1825) and *Drypta longicollis* MacLeay from the Natural History Museum (NHM) in London and MNHN and determined that the specimens from Yunnan were identical with *Desera unidentata* (MacLeay) (Fig. 2) specimens.



Habitus and Labels of Type Specimens (scale lines = 2.0 mm)

FIGURE 1 (above). Lectotype of *Drypta longicollis* MacLeay, 1825 (from India).  
FIGURE 2 (below). Holotype of *Drypta unidentata* MacLeay, 1825 (from Java).

The fact that *Drypta longicollis* MacLeay is actually a member of genus *Drypta* Latreille, and not of *Desera* Dejean, is also problematic because *D. longicollis* is the type species of *Desera* Dejean. The valid generic name for the species with pectinate tarsal claws, currently included in genus *Desera*, needs to be established.

The purposes of this paper are: (1) to establish the valid generic name for the species currently included in genus *Desera* Dejean; (2) to remove *Drypta longicollis* MacLeay from *Desera* and return it to genus *Drypta* Latreille, and (3) to provide additional descriptive information that will aid in the identification of specimens of both *Drypta longicollis* and “*Desera*” *unidentata*.

The abbreviations used in this paper are as follows: Ant 1 = antennomere 1 (scape); Ant 3 = antennomere 3; PL = length of pronotum measured along median line; PW = Widest width of pronotum; EL = length of elytra; and EW = widest width across both elytra.

### STATUS OF THE GENUS NAME *DESERA* DEJEAN

Latreille (1796:75) described genus *Drypta* but did not list any included species with his original description. He later designated *Carabus emarginatus* Gmelin (= *Carabus dentatus* P. Rossi) as type species (Latreille 1802). The status of *Drypta* Latreille as a valid genus is unquestioned.

In his description of *Drypta longicollis*, Dejean (1825:28) listed “*Desera Bonelliana*. Leach” as a synonym of that species, and, at the end of his description, he mentioned that Leach had established a distinct genus, *Desera*, for this species. Our review of Leach’s pertinent published works (Leach 1815 and 1817) and of his classification as reported by Samouelle (1819) failed to turn up any mention of a genus *Desera* or of a species, *Desera bonelliana*; so Dejean’s assignments must have been based on determinations in Leach’s collection and not on a published account. Hope (1831:21) briefly described *Desera nepalensis*, but failed to note the presence of pectinate tarsal claws in this species. Later (Hope, 1838), he cited Leach as the author of *Desera* and designated *Cicindela cylindricollis* Fabricius (= *Carabus distinctus* P. Rossi) as the type species of the genus. In a subsequent brief description of *Desera*, Hope (1838:105) once again omitted any mention of pectinate tarsal claws. His apparent failure to appreciate this distinguishing feature of true “*Desera*” species probably accounts for his selection of a true *Drypta*, *D. distincta* (Rossi), as his type species for *Desera*.

The authorship of genus *Desera* has remained a point of contention; some authors (e.g., Bousquet 2002; Löbl and Smetana 2002) cite Dejean (1825) as the author, others (e.g., Csiki 1932; Andrewes 1939; Lorenz, 1998b) credit Hope (1831). If Hope is the author, based on his use of the name in 1831, then *Desera nepalensis* is the type species of *Desera* by monotypy. If his claim of authorship were based on his 1838 paper, with his designation of *Cicindela cylindricollis* Fabricius as type species, then *Desera* would be a subjective junior synonym of *Drypta* Latreille, as was suggested by Andrewes (1939). In fact, Bousquet (2002) has settled the argument to our satisfaction, citing Dejean as author, with Article 11.6 of the 1999 International Code of Zoological Nomenclature as the justification, and with *Drypta longicollis* MacLeay as type species by monotypy. This means that *Desera* Dejean is a junior subjective synonym of *Drypta* Latreille.

In 1846, Schmidt-Göbel described the genus *Dendrocellus*, listed distinguishing features, including the presence of pectinate tarsal claws, and included three species. Two of these were described as new. The first, *Dendrocellus discolor*, is now recognized as a junior synonym of *Desera nepalensis* Hope. The second, *Dendrocellus flavipes*, which Schmidt-Göbel had misidentified as *Drypta flavipes* Wiedemann and transferred to his new genus, is conspecific with and a junior synonym of *Drypta geniculata* Klug. The third species was *D. geniculata* Klug itself. Schmidt-Göbel did not designate one of these as type species.



Chaudoir (1861:545) first included *Drypta longicollis* MacLeay in *Dendrocellus*, and several other workers followed (Bates 1892; Andrewes 1919 and 1936; Winkler 1924; Jedlička 1963; and Hansen 1967). Dupuis (1912) cited *Dendrocellus* as a subgenus of *Desera* in his description of *Desera gilsoni* from Taiwan. Andrewes (1939:133) synonymized *Desera* with *Drypta*, based on Hope's (1938) type species designation, recognized *Dendrocellus* as a valid genus name, and selected *D. discolor* (= *Desera nepalensis* Hope) as type species. However, *Dendrocellus* has been treated as a junior synonym of *Desera* Dejean (or Hope) by most recent workers (e.g., see Lorenz, 1998b; and Löbl and Smetana, 2003).

Our conclusion that the type species of *Desera* Dejean (i.e., *Drypta longicollis* MacLeay) should be included in *Drypta* leads us to join Andrewes (1939) in treating *Desera* Dejean (not Hope) as a synonym of *Drypta* Latreille and *Dendrocellus* Schmidt-Göbel as the valid name for the species with pectinate tarsal claws formerly included in *Desera* Dejean (or Hope [see above]).

### SPECIES REDESCRIPTIONS

#### *Drypta longicollis* MacLeay, 1825

(Figs. 1, 3–4)

*Drypta longicollis* MacLeay, 1825:28 (India)

*Drypta longicollis* Dejean, 1825:185 (India).

*Dendrocellus longicollis* Dejean; Bates, 1892:385 (Burma).

*Desera longicollis* MacLeay; Jedlicka, 1963:486 (Burma, India).

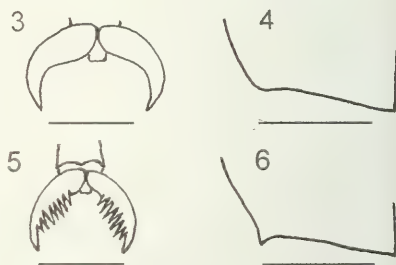
**SPECIMENS EXAMINED.**—Lectotype (Fig. 1), a male (MNHN), "Type, Coll. Dejean", "Ex Museo, Chaudoir"; "*longicollis* Dej., Indes Orient."; paralectotype, 1 female (MNHN), "Ex Museo, Chaudoir", "*longicollis* Dej., Indes Orient." Both lectotype and paralectotype are designated here.

**DESCRIPTION.**—Tarsal claws in type specimens simple (Fig. 3) and outer angle of each elytron round (Fig. 4). Ant 1 with basal third brown, apical two-thirds black. Ratio Ant 1 : Ant 3 = 4.20 (paralectotype); ratio PL : PW = 1.65 (lectotype), 1.64 (paralectotype); ratio EL : EW = 1.74 (lectotype), 1.78 (paralectotype); ratio EW : PW = 2.30 (lectotype), 2.29 (paralectotype). For additional morphological characteristics, refer to Dejean's description (1825: 185–186).

**DISTRIBUTION.**—India and Myanmar (= Burma).

**REMARKS.**—*Drypta longicollis* was described by both MacLeay and Dejean in 1825, based on the same specimens (in Dejean's collection) from India (MacLeay 1825:28; Dejean 1825:185). MacLeay's work was several months earlier than Dejean's, and therefore this species name is attributed to MacLeay (Andrewes 1919:134).

Considering his generally excellent work on the carabids of Middle and Southeast Asia, it is strange that Andrewes, after examination of the type of *Drypta longicollis* MacLeay, still mistreated it as representing a *Desera* species. He also misidentified specimens of *Dendrocellus unidentatus* (MacLeay) as *Drypta longicollis* MacLeay (see "Specimens examined" below).



FIGURES 3–4. *Drypta longicollis* MacLeay, 1825 (lectotype, from India): (3) fore-tarsal claws; (4) outer angle and sutural angle of left elytron.

FIGURES 5–6. *Drypta unidentata* MacLeay, 1825 (holotype, from Java): (5) fore-tarsal claws; (6) outer angle and sutural angle of left elytron.

Scale bars = 0.24 mm in Figs. 3 and 5 and 1.00 mm in Figs. 4 and 6.

***Dendrocellus unidentatus* (MacLeay), 1825, new combination**

(Figs. 2, 5–6)

*Drypta unidentata*, MacLeay, 1825:28 (Java).*Desera unidentata* (MacLeay), Andrewes, 1919:167 (Java)*Dendrocellus longicollis* Dejean; Chaudoir, 1861: 45 (India).*Desera longicollis* MacLeay; Andrewes, 1936:136 (India).*Desera longicollis* Dejean; Hansen, 1967:403 (Laos).

**SPECIMENS EXAMINED.**— Total 15 specimens. Holotype, 1 female (NHM), “*unidentata* Mac.”, “Java, Horsfield, 60-15”, “60-15, E.I.C.”, “Type, H.T.”, “58”, “54”; 1 specimen (NHM, sex status undeterminable), “Bonvouloir collection”, “*Desera unidentata* MacLeay, compared with type H.E.A.”, “*unidentata* Macleay (*Dendrocellus*) Schmidt-Goebel, Java”, “H.E. Andrewes coll., B. M. 1945-97”; 1 female (NHM), “Dammerman, N.W. Seomba, Laora 100M, 104 IV 1925”, “Ex Mus., Buitenzurg”, “*Desera unidentata* MacL., H.E. Andrewes det.”; 1 male (NHM), “Andaman Is., 1915-38”, “Ex Coll., Brit. Mus.”, “*Desera longicollis* Dej. (See back), compared with type, H.E.A., [on the back of the label] in type the angle of truncure is not dentate”; 1 male (NHM), “Annam, Keng trap, May 1917, R.V. de Salvaza”, “*Desera longicollis* Dejean, H.E. Andrewes det.”, “H.E. Andrewes Coll., B.M. 1945-97”; 1 female (NHM), “47252”, “Captn Wimberley”, “Andaman Islands”, “Fry Coll., 1905.100”, “*Desera longicollis* Dej., H.E. Andrewes det.”, “*Dendrocellus longicollis* Dej., Andaman Is.”; 1 female (MNHN), “Malacca, H. Deyrolle”, “Ex Museo, Chaudoir”, “*unidentata*, Java, C. Gary, Reiche”; 1 male (MNHN), “Java”, “Ex Museo, Chaudoir”, “*unidentata*, Java, C. Gary, Reiche”; 2 females (MNHN), “Ex Museo, Chaudoir”, “*unidentata*, Java, C. Gary, Reiche”; 1 male (IOZ), “China, Yunnan Province, Nujiang Prefecture, Lushui County, Liuku Township, Liuku, 800m”, N25.86010°, E98.85155°, 25-26 June 2000, Stop #00-7, D.H. Kavanaugh & H.-B. Liang collectors”; 1 male and 2 females (IOZ), “Yunnan, Mengla”, “20 April 1982, Peiyu Yu collector, by light trap”; 1 female (IOZ), “Yunnan, Xishuangbanna, Xiaomengyang, 850m”, 25 April 1987, Shuyong Wang collector”.

**DESCRIPTION.**— Because Andrewes (1919:167–168) gave a quite detailed redescription, we simply add the following: Ratio Ant 1 : Ant 3 = 3.67 (type), 3.26–3.56 (others); ratio PL : PW = 1.62 (type), 1.50–1.76 (others); ratio EL : EW = 1.67 (type), 1.70–1.82 (others); ratio EW : PW = 2.47 (type), 2.24–2.52 (others).

**DISTRIBUTION.**— Indonesia (Java), India (Andaman Is.), Vietnam (central), and China (Yunnan).

**REMARKS.**— Specimens of *Dendrocellus unidentatus* (MacLeay) can be distinguished from those of all other known *Dendrocellus* species by the following combination of character states: femora brown except for apices (black), tibia black, outer angles of elytra strongly dentate (Fig. 6), elytra widened posteriad, elytral intervals densely punctate, tarsal claws markedly pectinate with length of individual pectinations (“teeth”) subequal to width of base of tarsal claw (Fig. 5). Andrewes (1919:167) gave a redescription of this species; but there are several errors included, namely: 1) this species was reported as restricted to Java (but present materials indicate that its distribution extends from Java north to India, Laos, Vietnam, and China); 2) antennomere 3 was described as having its base and apex red and separated by a black subapical ring (but in all specimens we examined, the basal half of this antennomere was blackish brown and its apical half brown); 3) the prothorax was described as nearly twice as long as wide (but it is only 1.50–1.75 times as long as wide among specimens we have seen); and 4) the tarsal claws were described as finely pectinate (but they are markedly pectinate in all specimens that we examined).

## ACKNOWLEDGMENTS

The authors thank Dr. Thierry Deuve (MNHN) and Ms. Christine Taylor (NHM) for loans of specimens. Thanks are also due to Dr. Yves Bousquet (Eastern Cereal and Oilseed Research Centre, Canada) and Mr. Paul Marek (California Academy of Sciences), for providing essential literature, to Boris Kataev (Institute of Zoology, St. Petersburg) for alerting us to a potential problem with the generic name, *Desera*, and to Professor Peiyu Yu (IOZ) for reviewing a draft of this paper. Photographs of habitus were taken by senior photographer Guoqing Mai (IOZ). This work was supported by National Natural Science Foundation of China (Grant No. 30000026) and U.S. National Science Foundation (Grant No. 0103795). This paper represents contribution no. 23 of the China Natural History Project of the California Academy of Sciences.

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## Two new Scorpionfishes (Scorpaenidae) from the South Pacific

John E. Randall<sup>1,3</sup> and David W. Greenfield<sup>2,3</sup>

<sup>1</sup> Bishop Museum 1525 Bernice St., Honolulu, Hawaii 96817-2704; <sup>2</sup> Department of Ichthyology, California Academy of Sciences, 875 Howard Street, San Francisco, California 94103.

*Scorpaenopsis eschmeyeri*, formerly tentatively identified as *S. possi*, is described as new from 17 specimens from Fiji, Chesterfield Islands in the Coral Sea, New Caledonia, and the southern Great Barrier Reef. It is separated from *S. possi* by the lack of the pretympenic spine that is unique to *S. possi*, by its smaller size (largest specimen, 142 mm SL, compared to 194 mm for *S. possi*), and by a longer head, snout, upper jaw, and predorsal length, compared to specimens of *possi* of the same size range. *Scorpaena lacrimatus* is described from a single specimen, 198 mm SL, taken in 400 m off Tahiti, Society Islands. It is distinct from other species of the genus by the combination of the following characters: deep body (depth 2.5 in SL), 17 pectoral rays, and 61 scales in longitudinal series.

Scorpionfishes, aptly named for their venomous fin spines, are not well represented at islands of the South Pacific, compared to the rest of the Pacific. Only 60 species of scorpaenids are known from the South Pacific from Lord Howe Island and New Caledonia to Easter Island (Solomon Islands and Vanuatu not included). By contrast, Poss in Carpenter and Niem (1999) listed 131 scorpaenids (12 with a question mark) for the central and western Pacific (Hawaiian Islands not included).

The Indo-Pacific scorpionfish genus *Scorpaenopsis* was revised by Randall and Eschmeyer (2001); 24 species were recognized, of which eight were described as new. One of these, the wide-ranging *S. possi*, included ten specimens from the southwest Pacific from Fiji to the southern Great Barrier Reef that lack the characteristic small spine (called the pretympenic spine) dorsally on the head before the tympanic spine. No typical *S. possi* were found at any of these localities. These ten specimens were not listed as paratypes of *S. possi*. Recent collections of shore fishes in Fiji by the authors and associates resulted in 12 additional specimens of the same form. Our study of these specimens, plus seven of the nontype “*possi*” (one CAS lot of three specimens from the Great Barrier Reef has been lost) has enabled us to determine that they represent a new species.

The Bishop Museum received a specimen of *Scorpaena* from Tahiti, caught at the unusual depth of 400 m. Four species of *Scorpaena* are reported from South Pacific islands of Oceania west to Australia: *S. thomsoni* Günther from Juan Fernandez Island, *S. orgila* Eschmeyer and Allen from Easter Island, *S. cookii* Günther from the Kermadec Islands to New South Wales, and *S. cardinalis* Richardson and *S. papillosa* (Forster) from New Zealand and southeastern Australia. In addition, *S. thomsoni* Günther was described from Juan Fernandez Island in the eastern Pacific. Comparison of the Tahitian specimen with these species, as well as others from the Indo-Pacific region, revealed that it represents an undescribed species.

The objective of the present paper is the description of these two new scorpionfishes.

<sup>3</sup> Research Associate, Department of Ichthyology, California Academy of Sciences.

## MATERIALS AND METHODS

Type specimens of the new *Scorpaenopsis* have been deposited at the following institutions: Australian Museum, Sydney (AMS); Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS); Museum National d'Histoire Naturelle, Paris (MNHN); National Science Museum, Tokyo (NSMT); and the U.S. National Museum of Natural History, Washington, D.C. (USNM).

Lengths of specimens are given as standard length (SL), measured from the front of the upper lip to the base of the caudal fin (posterior end of the hypural plate); head length is measured from the same anterior point to the posterior end of the opercular membrane; body depth is the maximum depth from the base of the dorsal spines (as they emerge from the body), and body width the greatest width just posterior to the gill opening; orbit diameter is the greatest bony diameter, and interorbital width the least bony width; upper-jaw length is taken from the front of the upper lip to the posterior end of the maxilla; caudal-peduncle depth is the least depth, and caudal-peduncle length the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of fin spines and rays are measured to their extreme bases; length of base of dorsal fin is measured from the front of the base of the first dorsal spine to the rear base of the last dorsal ray (not to the end of the membrane connecting ray to caudal peduncle); pectoral-fin length is the length of the longest ray. Morphometric data presented in Tables 1 and 2 are given as percentages of the standard length. Proportional measurements in the text are rounded to the nearest 0.05. Pectoral-ray counts include the slender uppermost unbranched ray; counts were made of the rays on both sides. The scales in longitudinal series on the body were counted as oblique rows from the upper end of the gill opening to the base of the caudal fin. Counts of gill rakers were made on the first gill arch, the raker at the angle is contained in the lower-limb count.

*Scorpaenopsis eschmeyeri* Randall and Greenfield, sp. nov.

Figs. 1–2; Table 1

**MATERIAL EXAMINED.**— HOLOTYPE: CAS 218804, female, 101.5 mm, Fiji, Vanua Levu, Rabi Island, northwest shore, 16°26.701'S, 179°56.261'W, 25 m from rocky shore, fringing reef, 1–2 m, rotenone, D.W. Greenfield, T.A. Greenfield, R.C. Langston, and J. Pilippoff, 20 May 2003. PARATYPES: CAS 214577, 115 mm SL, Australia, Queensland, Great Barrier Reef, Capricorn Group, One Tree Island, off reef crest on west side just above dropoff, rotenone, V.G. Springer, 7 December 1966; USNM 243332, 108.0 mm, Fiji, Malolo Island, south side of channel at northwest end of island barrier reef, sand channels and rock walls, 0–18 m, rotenone, V.G. Springer et al., 25 May 1982; USNM 259405, 84.0 mm, Fiji, Viwa Island, small islet on Viwa Reef (17°11'S, 176°54'E), rotenone, V.G. Springer et al., 27 May 1982; BPBM 33775, 75.5 mm, Coral Sea, Chesterfield Islands, lagoon, south end, patch reef, 2–4 m, rotenone, M. Kulbicki, J.E. Randall, P.J. Doherty, and C. Goiran, 29 August 1988; BPBM 34264, 2: 64.7–65.5 mm, New Caledonia, lagoon near southeast end of St. Vincent Pass, 22°2.1'S, 165°57.8'E, reef in 2–4 m, rotenone, M. Kulbicki, J.E. Randall et al., 21 March 1990; NSMT-P 67891, 101.0 mm SL, Fiji, Viti Levu, barrier reef off Suva, main channel between wreck and end of reef, 18°8.90'S, 178°23.91'E, spur and groove, 4.5–8 m, rotenone, D.W. Greenfield, K.R. Longnecker, and K.S. Cole, 31 May 1999; BPBM 39423, 63.0 mm SL, same locality as preceding, spur and groove, 12–18.5 m, rotenone, D.W. Greenfield, K.R. Longnecker, K.S. Cole, and R.C. Langston, 27 January 2002; CAS 219133, 2: 27.0–45.5 mm, Fiji, Viti Levu, barrier reef off Suva, fish patch, backside of dropoff towards reef, 18°9.59'S, 178°23.96'E, 7.5–10.5 m, rotenone, D.W. Greenfield, K.R. Longnecker, K.S. Cole, and



R.C. Langston, 2 February 2002; USNM 375892, 94.0 mm, Fiji, nearly the same locality as preceding, 18°9.545'S, 178°23.974'E, 8.5–15 m, same collectors, rotenone, 3 February 2002; AMS I.42980-001, 79.0 mm, Fiji, Viti Levu, off Suva, Makuluva Island, west side, 18°11.227'S, 178°31.040'E, edge of cut in reef, very silty, 3–5 m, same collectors, rotenone, 4 February 2002; BPBM 39424, 2: 38.5–95.5 mm, Fiji, Viti Levu, off Suva, outside barrier reef about 1 mile west of sand bank cut, 18°11.161'S, 178°26.757'E, spur and groove, but mostly coral, 12 m, rotenone, D.W. Greenfield and K.S. Cole, 9 February 2002; CAS 219135, 107 mm, same locality as BPBM 39424, 14–15 m, rotenone, K.R. Longenecker and R.C. Langston, 9 February 2002; CAS 219134, 28 mm, Fiji, Viti Levu, off Suva, outside barrier reef, about 1 mile west of sand bank cut, 18°11.163'S, 178°26.28'E, sandy hole in reef surrounded by coral (mostly dead), 23–24 m, rotenone, D.W. Greenfield, K.R. Longenecker, K.S. Cole, and R.C. Langston, 10 February 2002; MNHN 2004-01171, 97.0 mm, Fiji, Northern Lau Group, Vanua Balavu Island, north side of island at Balavu Harbor, 17°11.212'S, 179°0.095'W, outside barrier reef, sand under an overhang, 12–15 m, rotenone, D.W. Greenfield, K.R. Longenecker, R.C. Langston, and Bio Koroï Mataitini, 8 January 2003.

**DIAGNOSIS.**—Dorsal rays XII,9; anal rays III,5; pectoral rays 17–18 (rarely 18); longitudinal scale series 44–48 (modally 46); body depth 2.8–3.05 in SL; head length 2.2–2.3 in SL; snout length 3.0–3.15 in head length; orbit diameter 4.65–4.95 in head length; nearly one-half of orbit extending above dorsal profile of head; interorbital width 6.75–7.2 in head length; pair of interorbital ridges flaring posteriorly, then curving medially to join slight incurved ridge at front of occipital pit; median interorbital ridge extending half way back in interorbital space; occipital pit shallow and not flat; no coronal spines; no pretympanic spines; suborbital pit not well developed; suborbital ridge with four spines, the first on lacrimal; two ventral spines on lacrimal, one directed mainly anteriorly and the other curving posteriorly; first dorsal spine 1.9–2.4 in second spine; third dorsal spine longest, 2.2–2.7 in head length; eleventh dorsal spine 1.55–2.0 in twelfth spine; second anal spine 1.65–2.0 in head length; no supraoccipital tentacle; color variable, the darkest blotches usually above tip of upper opercular spine, two on lateral line, two obliquely above and forward of these, two in soft portion of dorsal fin, and one in anal fin. Largest type specimen, 115 mm.

**DESCRIPTION.**—Dorsal rays XII,9; anal rays III,5; all dorsal and anal soft rays branched, the last to base; pectoral rays 17 (17, two of 28 counts are 18), the second to fourth branched (second to fourth, fifth, or sixth branched in paratypes); pelvic rays I,5, all soft rays branched; principal caudal rays 13, the middle 11 branched; upper and lower procurent caudal rays 7, the most posterior segmented; lateral-line scales 22 (22–23), plus two on base of caudal fin, the first at upper end of gill opening spinous, the next few progressively less so; longitudinal scale series 46 (44–48; one of 14 with 44, three with 45, six with 46, three with 47, and one with 48); scales above lateral line to middle of dorsal fin 8; scales below lateral line to origin of anal fin about 16; median predorsal scales about 9; circumpeduncular scales about 25; gill rakers 5 + 9; pseudobranchial filaments of holotype 31 (26 for 79-mm paratype); vertebrae 24.

Body depth 2.8 (2.55–3.05) in SL; body width 1.4 (1.25–1.6) in body depth; head length 2.2 (2.2–2.3) in SL; snout length 3.15 (3.0–3.05) in head length; orbit diameter 4.8 (4.65–5.2) in head length; nearly one-half of orbit extending above dorsal profile of head; interorbital space deeply concave, the least width 6.75 (6.8–7.35) in head length; caudal-peduncle depth 3.65 (3.7–3.95) in head length; caudal-peduncle length 3.1 (2.95–3.6) in head length.

Mouth moderately large, the maxilla extending to a vertical at posterior edge of pupil, the upper-jaw length 2.0 (1.9–1.95) in head length; lower jaw projecting; mouth oblique, forming an angle of about 25° to horizontal axis of body; upper jaw with a dense band of small, slender, con-



FIGURE 1. Holotype of *Scorpaenopsis eschmeyeri*, CAS 218804, female, 101.5 mm, Fiji (D.W. Greenfield).

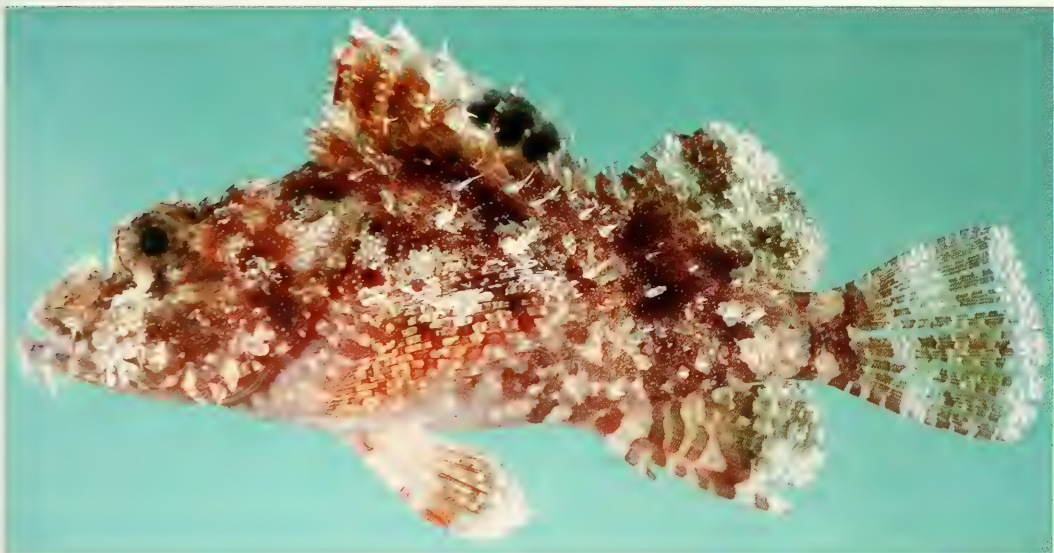


FIGURE 2. Paratype of *Scorpaenopsis eschmeyeri*, BPBM 33775, male, 75.5 mm, Chesterfield Islands, Coral Sea (J.E. Randall).

ical, incurved, and inwardly depressible teeth in about six to seven rows, narrowing to two or three rows posteriorly, the symphyseal gap at front of jaw about one-third pupil diameter in width; lower jaw with a similar band of teeth in about five or six rows anteriorly, narrowing to one or two posteriorly; three irregular rows of small, slender, incurved, conical teeth forming a V on vomer; no teeth on palatines. Tongue short, very thick and broadly rounded, with a slender rod-like median anterior projection. Gill rakers short, with small spinules, the longest at angle, equal in length to longest gill filaments.

Head spination typical of the genus; no coronal spines; pair of interorbital ridges flaring posteriorly, then curving medially to join slight incurved ridge at front of occipital pit; median interorbital ridge extending half way back in interorbital space; occipital pit shallow and not flat; tympan-



ic spines about equal in length to postocular spines; parietal, and nuchal spines strongly recurved, sharing a broad base; three very small sphenotic spines, followed by the pterotic, lower posttemporal and supracleithral spines; upper posttemporal spine very small; no developed postocular spines; nasal spines small; suborbital pit between anterior part of orbit and large bony knob on lacrimal not deep; suborbital ridge with four spines, the first on lacrimal more erect; lacrimal with a dorsoanterior ridge, an anterior ridge (without a sharp anterior tip), and two ventral spines, one strongly directed anteriorly and the other curving posteriorly; two opercular spines, the upper flat, without a ridge, the lower preceded by a slightly curved ridge with a short ridge above and adjacent to its base; four preopercular spines, the uppermost with an anterior supplemental spine, the lowermost very short; clavicular spine strong, projecting dorsoposteriorly, without a median ridge.

No supraocular tentacle; a small tentacle associated with anterior ventral spine of lacrimal and two large flat fimbriate tentacles following posterior spine; a series of four small cutaneous flaps on lower jaw just below lower lip; a few small flaps on lower edge of preopercle and three slender ones posteriorly on upper part of maxilla; body with very small scattered cutaneous flaps; lateral line with flaps on fourth, sixth, ninth (largest), thirteenth, sixteenth (small), and twentieth scales.

Anterior nostril below base of nasal spine, with a posterior fimbriate flap about twice as long as spine; posterior nostril at edge of orbit below preocular spine, with a low fleshy rim.

Scales on body ctenoid, becoming cycloid ventrally on abdomen, chest, and prepectoral area, extending onto base of pectoral fins in a broad V-shape; cycloid scales basally on opercle, including a few embedded scales above base of ridge of lower spine; scales on opercular flap between opercular spines; no scales on fins except three vertical rows on base of caudal fin.

Origin of dorsal fin above supracleithral spine, the predorsal length 2.45 (2.3–2.5) in SL; first dorsal spine 2.2 (1.9–2.4) in second spine, 7.1 (6.2–7.35) in head length; third dorsal spine longest, 2.7 (2.2–2.65) in head length; eleventh dorsal spine 1.75 (1.55–2.0) in twelfth spine; last dorsal soft ray joined by membrane to dorsal edge of caudal peduncle above base of penultimate lateral-line scale; origin of anal fin below base of first dorsal soft ray, the preanal length 1.4 (1.35–1.4) in SL; first anal spine 4.1 (3.5–4.2) in head length; second anal spine much longer than third, 2.0 (1.65–1.9) in head length; first anal soft ray longest, 1.9 (1.5–2.0) in head length; caudal fin slightly rounded, 1.6 (1.55–1.65) in head length; sixth and seventh pectoral rays longest, 1.45 (1.35–1.6) in head length; origin of pelvic fins below base of third dorsal spine (hence distinctly posterior to base of pectoral fins), the prepelvic length 2.5 (2.5–2.6) in SL; pelvic spine 2.7 (2.4–2.8) in head length; pelvic fins approaching or extending slightly posterior to anus, the second ray longest, 1.6 (1.5–1.7) in head length.

*Color of holotype in alcohol:* body brownish gray, becoming white on abdomen and chest, with six irregular blackish blotches along back, progressively smaller posteriorly, a black spot above clavicular spine, and less distinct blackish blotches along or near lateral line; ventral part of body from above anus to base of caudal with irregular near-white blotches, the largest lightbulb-shape on lower half of caudal peduncle; head brownish gray, pale ventrally, with light gray-brown blotches; a black spot on opercular membrane above upper opercular spine, and another on lower part of opercle below level of upper preopercular spine; a large dark blotch above and posterior to upper corner of maxilla; maxilla blotched with white; lips crossed with dark gray-brown spots; spinous portion of dorsal fin mottled gray and whitish, the soft portion gray along about basal third, whitish on outer two-thirds, with two slightly oblique blackish cross bands, the more anterior the most distinct; anal fin white with four irregular oblique dark bands, the third darkest; caudal fin pale with four or five brownish gray spots forming irregular bars; pectoral fins pale gray-brown, whitish distally, with irregular dark brownish gray cross bands; pelvic fins whitish with a few faint gray blotches on outer part of first four soft rays.



TABLE 1. Proportional measurements of type specimens of *Scorpaenopsis eschmeyeri* expressed as percentages of the standard length.

	CAS	CAS	BPBM	BPBM	AMS I.	USNM	BPBM	NSMT-P	CAS
	218804	219133	34264	33775	42980	375892	39198	67891	214577
Sex	female	immature	male	male	female	female	female	female	female
Standard Length (mm)	101.5	45.5	65.5	75.5	79	94	95.5	101	115
Body depth	35.7	32.8	33.8	35.2	33.7	33.7	34.5	34.2	39.4
Body width	25.9	22	22.6	24.1	25.2	26.7	24.6	23.8	24.7
Head length	45.3	43.8	44	44.6	43.9	44.7	44.8	45.5	45.5
Snout length	14.3	14.5	14.6	15.2	14.3	14.6	14.6	14.8	15
Orbit diameter	9.3	9.2	9.2	9.3	8.9	9.6	9.6	9.5	8.8
Interorbital width	6.7	6.6	6.3	6.1	6.2	6.6	6.5	6.6	6.2
Caudal-peduncle depth	12.4	11.5	11.5	11.9	11.7	11.7	12.1	11.5	12.3
Caudal-peduncle length	14.7	14.5	13.5	13.9	14.9	14.3	12.6	12.9	12.7
Upper-jaw length	22.9	22.2	22.3	23.7	22.8	22.9	23.1	23.7	23.4
Predorsal length	41	40	39.9	40.4	40.2	40.5	41.5	41.7	40.5
Preanal length	72.5	72.2	71	70.8	71.3	72.6	72.8	73	72.7
Prepelvic length	40.1	39.2	38.3	39.7	38.8	39	39.3	39.7	41.1
Dorsal-fin base	57.2	56.4	55.2	57.6	58.6	57	55.1	55.2	57.9
First dorsal spine	6.4	7.1	7	6.8	6.8	6.9	7.2	6.2	7.1
Second dorsal spine	13.3	17.1	14.9	14.8	14	13.9	13.8	14	14.9
Longest dorsal spine	16.7	19.8	18.7	19.6	18.3	18.1	18.3	17.1	18.4
Eleventh dorsal spine	7.9	7.7	7.7	8	7.6	8.5	8.4	9	8.2
Twelfth dorsal spine	13.8	14.5	14.3	15.2	15.1	13.9	14.6	13.9	14.1
Longest dorsal soft ray	18.9	19.8	19.9	20.2	18	18.4	19.9	18.5	19.6
Anal-fin base	14.5	15.9	14.8	16.4	16.8	15.6	14.7	15	14.5
First anal spine	10.8	11.4	10.5	12.1	12.6	10.7	12	10.9	12.4
Second anal spine	22.6	24.8	26.7	27.1	25.9	24.2	25.2	23.8	25.3
Third anal spine	19.3	20.4	21.7	21.2	21.4	20.1	21.2	19.4	19.4
Longest anal soft ray	24.1	24.5	26.8	24.9	24.8	23.5	24	23	23.3
Caudal-fin length	27.8	28.7	29.3	29.2	27.8	27.7	27.6	27.6	28.4
Pectoral-fin length	31	32.6	30.7	31.8	31.4	30.9	30.7	28.7	29.6
Pelvic-spine length	16.7	17.3	17.5	18.7	16.7	15.6	16.9	16.4	17
Pelvic-fin length	27.8	28.3	28.1	27	29	28.2	27.2	26.5	27

*Color of holotype when fresh:* body above pectoral fin to below ninth dorsal spine mottled red-dish brown, becoming mottled reddish gray posteriorly to caudal peduncle where irregularly marked with pale red and dark reddish brown; dark brown blotches more conspicuous than on pre-served specimen; cutaneous flaps dorsally on body and on lateral line pale bluish gray, those on lower side pale tan with white edges; abdomen pale salmon; head mottled brownish red, pale orange-red ventrally and on chest and lower part of prepectoral area; head, body, median fins, and upper part of pectoral fins with numerous white dots, many grouping to form irregular markings;

areas of dorsal and anal fins indicated as pale in preservative were light red when fresh; caudal-fin membranes transparent, the rays banded with pale red and dark reddish brown; pectoral fins similar in color to caudal fin, the lower ten rays more banded in light red; pelvic fins with a large circular light red area covering most of outer three-fifths of fin, the margin white, the base pale salmon.

**ETYMOLOGY.**— Named in honor of William N. Eschmeyer in recognition of his research on the Scorpaenidae.

**REMARKS.**— In their revision of *Scorpaenopsis*, Randall and Eschmeyer (2001:59) listed seven lots of the genus from Fiji, New Caledonia, Chesterfield Islands in the Coral Sea, and One Tree Island of the Capricorn Group, southern Great Barrier Reef as nontype specimens of *S. possi*. These specimens lack the pretympanic spine that is unique to *S. possi*. No typical specimens of *S. possi* were found at any of these localities. Randall and Eschmeyer suggested that these specimens represent a southwestern population of *S. possi* in the Pacific. Our additional 12 specimens from Fiji, 27–108 mm SL, provided for more comparison with *S. possi* and the conclusion that this population represents a new species.

Our first suspicion that the specimens from the southwest Pacific represent a new species was noting their small size compared to *S. possi*, with mature females as small as 79 mm SL. Twenty specimens of *S. eschmeyeri* are 142 mm SL or less (these include the lot of three uncataloged CAS nontype specimens of *S. possi* listed by Randall and Eschmeyer, which have been lost). Nineteen of these are 117 mm SL or less. Seventy type specimens of *S. possi* are larger than 117 mm SL, and 18 range from 142–194 mm SL, the largest from Rarotonga, Cook Islands.

The 142-mm specimen of *S. eschmeyeri* is one of two specimens from the Capricorn Group of the southern Great Barrier Reef listed as nontypes of *S. possi* by Randall and Eschmeyer (then as CAS uncat.). The smaller specimen, 115 mm SL, is now CAS 214577. The larger specimen is tentatively identified as *S. eschmeyeri*, but it is not listed as a paratype because of its unusual large size compared to the other type specimens and because it was preserved with the mouth rigidly and fully open and the body curved, hence making accurate measurements difficult. It is cataloged separately as CAS 219194.

Although we found no meristic differences to separate *S. eschmeyeri* from *S. possi*, four measurements serve to differentiate the two species when comparing specimens of the same size range: head length, snout length, upper-jaw length, and predorsal length.

The head length of 10 Bishop Museum paratypes of *S. possi* from 59–121 mm SL is 42.5–43.4% SL, compared to 43.9–45.5% for 17 *S. eschmeyeri*. The snout length of *S. possi* is 13.4–14.2% SL (except BPBM 29332, 86 mm SL, from the Ryukyu Islands with 14.9%), compared to 14.3–15.9% for *S. eschmeyeri*. The upper-jaw length of *S. possi* is 20.6–22.5% SL, compared to 22.2–24.5% SL for *S. eschmeyeri*. The predorsal length of *S. possi* is 37.0–39.8% SL, compared to 39.9–42.1% SL for *S. eschmeyeri*.

The best character to separate the two species is the presence of pretympanic spines in *S. possi* (larger than about 60 mm SL) and their absence in *S. eschmeyeri*.

The two species are not known to coexist. *Scorpaenopsis possi* ranges from the Red Sea and east coast of Africa to the islands of French Polynesia except Rapa. The distribution in the western Pacific is from Taiwan to the Solomon Islands. *Scorpaenopsis eschmeyeri* is currently represented by specimens from Fiji, New Caledonia, the Chesterfield Islands in the Coral Sea, and the southern Great Barrier Reef.

*Scorpaena lacrimata* Randall and Greenfield, n. sp.

Fig. 3; Table 2

**MATERIAL EXAMINED.**— Holotype: BPBM 31706, female, 198.0 mm, Society Islands, Tahiti, 400 m, hook and line, Michel Kung (via Louise Wrobel), 24 October 1990.

**DIAGNOSIS.**— Dorsal rays XII,9; anal rays III,5; pectoral rays 17; longitudinal scale series 61; body depth 2.5 in SL; head length 2.15 in SL; snout length 3.2 in head length; orbit diameter 4.6 in head length; about one-third of orbit extending above dorsal profile of head; interorbital width 7.35 in head length; pair of interorbital ridges curving at front of occipital pit to join tympanic spines; median interorbital ridge extending half way back in interorbital space; occipital pit quadrangular and moderately deep; no coronal spines; no suborbital pit; suborbital ridge with four spines, the first on lacrimal; first dorsal spine 1.8 in second spine; third and fourth dorsal spines longest, equal to second anal spine, 2.35 in head length; eleventh dorsal spine 1.65 in twelfth spine; supraoccipital tentacle present; small tentacles associated with ventral spines of lacrimal; no tentacles or cutaneous flaps on chin or on body; a row of small teeth on palatines; pale yellowish in alcohol, with scattered small dark brown spots on head, body, and dorsal fin; a short, narrow, dark brown bar extending ventrally from middle of edge of orbit.

**DESCRIPTION.**— Dorsal rays XII,9; anal rays III,5; all dorsal and anal soft rays branched, the last to base; pectoral rays 17, the second to eighth branched; pelvic rays I,5, all soft rays branched; principal caudal rays 14, the median 12 branched, the lower simple rays thickened; upper and lower procurrent caudal rays 7, the posterior two segmented lateral-line scales 22, the first two spinous; longitudinal scale series 61; scales above lateral line to middle of dorsal fin 10; scales below lateral line to origin of anal fin 19; median predorsal scales about 9; circumpeduncular scales about 25; gill rakers 4 + 10; pseudobranchial filaments 52; vertebrae 24.

Body deep for the genus, the depth 2.5 in SL; body width 1.6 in body depth; head length 2.15 in SL; snout length 3.2 in head length; orbit diameter 4.6 in head length; about one-third of orbit extending above dorsal profile of head; interorbital space deeply concave, the least width 7.35 in head length; caudal-peduncle depth 3.9 in head length; caudal-peduncle length 3.1 in head length. Mouth terminal and large, the maxilla extending to below posterior edge of orbit, the upper-jaw length 2.0 in head length; mouth oblique, forming an angle of about 25° to horizontal axis of body; upper jaw with a dense band of small, slender, conical, incurved, and inwardly depressible teeth in about eight rows, narrowing to two or three rows posteriorly, the symphyseal gap at front of jaw one-half pupil diameter in width; lower jaw with a similar band of teeth in about six or seven rows anteriorly, narrowing to two rows posteriorly; a single row of small, slender, incurved, conical teeth forming a 'V' on vomer; similar teeth in a single row on palatines. Tongue thick and triangular with a fleshy rounded tip, the upper surface coarsely plicate. Gill rakers short, with spinules, the longest at angle nearly as long as longest gill filaments.

Head with the usual complement of head spines, most prominent and retrorse; no coronal spines; pair of interorbital ridges flaring posteriorly, each curving laterally at anterior edge of occipital pit to join tympanic spine; median interorbital ridge extending half way back in interorbital space; occipital pit quadrangular, flat, and moderately deep; tympanic, parietal, and nuchal spines broad-based and of about equal size; two sphenotic spines, followed by the pterotic, lower posttemporal (upper posttemporal directly above), and supracleithral spines; two very small postocular spines (only as small bumps on right side); no suborbital pit; suborbital ridge with four spines, the first on lacrimal more erect; lacrimal with four other spines, the first mainly a forward-directed ridge with a very short free tip; second and third spines directed dorsoventrally (the third clearly shortest), the last spine curving ventroposteriorly; two opercular spines, slender and not



divided, each preceded by a prominent ridge, the upper curved, and the lower slightly curved; five preopercular spines, the uppermost with a strong anterior supplemental spine, the lower two very short; clavicular spine strong, projecting dorsoposteriorly, with a slight median ridge.

A fleshy supraorbital tentacle about three-fourths orbit diameter in length between supraocular and postocular spines; a small slender tentacle ventrally at front of lacrimal, another at base of second ventral spine of lacrimal, and one with last lacrimal spine, broad and as long as spine; a few small tentacles on lower edge of preopercle, the largest with the fifth preopercular spine; no flaps or tentacles detected on chin or elsewhere on head and body.

Anterior nostril below base of nasal spine, with a posterior fimbriate flap longer than spine; posterior nostril at edge of orbit below preocular spine, with a slight membranous rim, the posterior edge with a few cirri.

Scales on body ctenoid, becoming cycloid ventrally on abdomen and on chest; prepectoral scales embedded; cycloid scales dorsally on opercle above upper spine; no scales on opercular flap above upper spine or below lower spine, but many on flap between spines; no scales on fins except three vertical rows on base of caudal fin.

Origin of dorsal fin above upper posttemporal spine, the predorsal length 2.7 in SL; first dorsal spine 1.8 in second spine, 5.1 in head length; third and fourth dorsal spines longest, 2.35 in head length; eleventh dorsal spine 1.65 in twelfth spine; second and third dorsal soft rays longest, 2.8 in head length; last dorsal soft ray joined by membrane to dorsal edge of caudal peduncle above base of penultimate lateral-line scale; origin of anal fin below base of twelfth dorsal spine, the preanal length 1.35 in SL; first anal spine 4.7 in head length; second anal spine slightly longer than third, 2.35 in head length; first and second anal soft rays longest, 1.6 in head length; caudal fin rounded, 2.2 in head length; ninth pectoral ray longest, 1.65 in head length; origin of pelvic fins posterior to base of pectoral fins, the prepelvic length 2.3 in SL; pelvic spine 2.45 in head length; pelvic fins extending posterior to anus, the second ray longest, 1.8 in head length.

*Color in alcohol:* pale yellowish with scattered dark brown spots, most on body no larger than scales, the most prominent on body above clavicular spine, above lower posttemporal and supraclithral spines, and as a curved transverse band across scaled part of nape; a short, narrow, dark brown bar extending ventrally from middle of orbit in line with a spot below second suborbital spine; a dark brown spot at convergence of opercular ridges; postorbital, sphenotic, and pterotic spines each in a dark brown blotch; occipital pit dusky with two small dark brown spots posteriorly; fourth interspinous membrane with a dusky blotch containing a vertically elongate dark brown

TABLE 2. Proportional measurements of holotype of *Scorpaena lacrimata* as percentages of the standard length

	BPBM 31706
Standard length (mm)	198.0
Body depth	40.3
Body width	25.3
Head length	46.4
Snout length	14.4
Orbit diameter	10.1
Interorbital width	6.3
Caudal-peduncle depth	11.6
Caudal-peduncle length	14.5
Upper-jaw length	22.5
Predorsal length	37.1
Preanal length	73.8
Prepelvic length	43.5
Dorsal-fin base	62.2
First dorsal spine	9.1
Second dorsal spine	16.3
Longest dorsal spine	19.7
Eleventh dorsal spine	9.6
Twelfth dorsal spine	15.6
Longest dorsal ray	16.4
Anal-fin base	16.1
First anal spine	9.9
Second anal spine	19.7
Third anal spine	18.2
Longest anal ray	28.7
Caudal-fin length	21.2
Pectoral-fin length	27.8
Pelvic-spine length	19.0
Pelvic-fin length	26.5

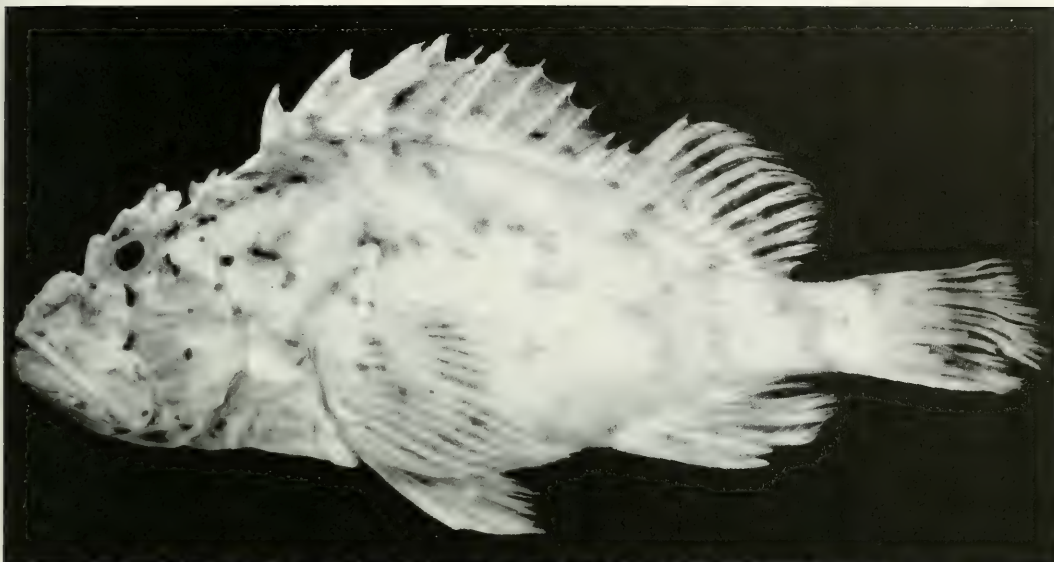


FIGURE 3. Holotype of *Scorpaena lacrimata*, BPBM 31706, 198 mm, Tahiti, 400 m (J.E. Randall).

spot; two dark blotches on fifth membrane and one on sixth, eighth, and ninth membranes; six small dark blotches on soft portion of dorsal fin, mainly on outer half; anal fin with two small dusky spots; caudal fin with dusky pigment on membranes forming a broad band across middle of fin; pectoral fins with two such transverse bands, one at base and one two-thirds out on fin; pelvic fin pale (one was removed).

**ETYMOLOGY.**— Named *lacrimata* from the Latin meaning to shed tears or weep, in reference to the short dark brown bar below the eye, reminiscent of a tear.

**REMARKS.**— No information was given on the color in life, but the fish was probably mainly red, in view of its capture in 400 m. The fins were pinned in erect position, and one pelvic fin was removed, suggesting that a photograph may have been taken, but none was provided.

Four other species of *Scorpaena* are known from islands of the South Pacific from Lord Howe Island to Easter Island. *Scorpaena lacrimata* differs from all in its greater body depth (2.5 in SL, compared to 2.7–3.1 for the mean depth of the four other species; data from Eschmeyer and Allen 1971 and Paulin 1982) and its count of 61 scales in longitudinal series. Paulin (1982) reported 48–50 scales for *S. cardinalis*, 64–67 for *S. cookii*, and 43–47 for *S. papillosa*. Eschmeyer and Allen (1971) counted 50–55 scales for *S. orgila*. The pectoral-ray count of 17 differentiates *lacrimata* further from *S. orgila* and *S. papillosa*, which have 15–16 pectoral rays. The chest of *S. lacrimata* is fully scaled, whereas that of *S. cookii* is naked and *S. cardinalis* has embedded scales.

Elsewhere in the Pacific, the genus *Scorpaena* is represented by two species in the Hawaiian Islands (Eschmeyer and Randall 1975), three in Japan (Nakabo 2002), two of which range to the south, and one in the Philippines (*S. hemilepidotus* Fowler). All are readily separated from *S. lacrimatus* by pectoral-ray counts except the two Hawaiian species, which differ in having 45 scales in longitudinal series, and *S. onaria* Jordan and Snyder from Japan, which has 17–19 (usually 17) pectoral rays (Motomura and Iwatsuki 1997); it is distinct in its low scale count and sharply descending anterior part of the lateral line.

Günther (1880:24, pl. 12) described *Scorpaena thomsoni* from the Juan Fernandez Island in the eastern Pacific off Chile. It seems to be the closest species to *S. lacrimata* from its color pat-

tern and general morphology. It differs in its lower count of scales in longitudinal series (Günther gave a count of 42, but his very good illustration shows 52), scaled prepectoral area (scales so embedded on *S. lacrimata* that scale outlines not readily seen), cutaneous flaps on body, a near-truncate caudal fin, and nine instead of ten lower pectoral rays unbranched.

#### ACKNOWLEDGMENTS

We thank Mme Louise Wrobel of Service de Ressources Marines of Papeete, Tahiti for providing the specimen of *Scorpaena lacrimata*, Loreen R. O'Hara of the Bishop Museum for X-rays, and the following persons for assistance in collecting fishes in Fiji: Kathleen S. Cole, Teresa A. Greenfield, Ross C. Langston, Kenneth R. Longenecker, Bio Koroi Mataitini, and Joanna Pilippoff. Captain Bruce Vasconcellos and the crew of *Moku Moku Hine* are gratefully acknowledged for their logistic support, as are Johnson Seeto, G. Robin South, Randolph R. Thaman, and Robert W. Tuxton of the University of the South Pacific for facilitating our collections in Fiji. We also thank the Fijian Government and local village chiefs for permission to collect fishes. This research was supported by NSF grants INT97-29666 and DEB01-02745 and Sea Grant Project R/FM-6PD.

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**The California Academy of Sciences  
Gulf of Guinea Expedition (2001)**

**I. The Taxonomic Status of the Genus *Nesionixalus* Perret,  
1976 (Anura: Hyperoliidae), Treefrogs of São Tomé and  
Príncipe, with Comments on the Genus *Hyperolius***

**Robert C. Drewes and Jeffery A. Wilkinson**

*Department of Herpetology, California Academy of Sciences,  
875 Howard Street, San Francisco, California 94103, USA;  
Email: rdrewes@calacademy.org; jwilkinson@calacademy.org*

The endemic hyperoliid treefrogs of São Tomé and Príncipe currently recognized as *Nesionixalus thomensis* (Bocage, 1986) and *N. malleri* (Bedriaga, 1892) are re-examined. The results of two molecular analyses indicate that these taxa are closely related to each other (monophyletic) but nest within the genus *Hyperolius*. A comparison of the morphological character states used by Perret (1976; 1988) to erect the genus *Nesionixalus* from within *Hyperolius* Rapp with a broad range of *Hyperolius* species reveals that most of these are not unique to the island endemics; all except the characters of size and digital tip shape are distributed among a number of other species within the latter genus. *Nesionixalus* Perret, 1976 is returned to the synonymy of *Hyperolius* Rapp and *Nesionixalus thomensis* and *N. malleri* to *Hyperolius thomensis* Bocage and *H. malleri* Bedriaga, respectively.

The islands of São Tomé and Príncipe (which together comprise the tiny African Republic of São Tomé e Príncipe) lie along a magmatic geological feature known as the Guinea Line (or Cameroon Volcanic Line), which is a flaw (or hotline — Meyers et al. 1998) in the African tectonic plate between 1000–1500 km long (Simkin et al. 1994; Burke 2001) that has served as a channel for magmas for millions of years. The Guinea Line extends across the ocean-continent transition, and magmatic extrusions up through it have given rise to major oceanic and continental topographic relief extending from southwest to northeast including the oceanic islands of Annobón (Pagalu; 4.9 my), São Tomé (13+ my), Príncipe (31+ my), the recent continental island of Bioko (known in colonial times as Fernando Poo and now part of the Republic of Equatorial Guinea), and the mainland features of Mount Cameroon, the various ranges that comprise the Cameroon Highlands, and the Jos Plateau of Nigeria (Lee et al. 1994). The islands of Annobón, Príncipe and São Tomé are oceanic islands in the sense of Darlington (1957), Carlquist, (1965) and MacArthur and Wilson (1967) and long known for the high levels of endemism in their biota; some taxa are shared between the latter two. The three islands are separated from each other and from the West African coastlines of Equatorial Guinea and Gabon by ocean depths in excess of 3000 m. Príncipe is geologically the oldest and only about 130 km<sup>2</sup> in area, but it is well-watered and has significant relief provided by a central volcanic peak of just under 1000 m. It is about 220 km southwest of Bioko, the only continental and most northerly island of the chain, about 220 km from the African

mainland, and approximately 146 km northeast of São Tomé. The latter is geologically younger than Príncipe and considerably larger, at 836 km<sup>2</sup>, with the central Pico do São Tomé rising to above 2000 m. São Tomé is situated 280 km off the mainland and 180 km northeast of the southern-most of the oceanics, tiny (17 km<sup>2</sup>) Annobón or Pagalu, which is part of the Republic of Equatorial Guinea. (Juste et al. 1994).

From late March to early June 2001, the California Academy of Sciences conducted a large, multi-disciplinary research expedition to both islands of the Republic of São Tomé e Príncipe (see Drewes 2002 for a popular account). Voucher specimens and tissues were collected of all of the amphibian and reptile species. This material allows us to address questions pertinent to both taxonomy and biogeography such as the status of the genus *Nesionixalus* relative to other genera in the family Hyperoliidae as well as to add natural history information based on our field observations. In this paper, we address the first issue.

The large, flamboyant treefrog, hitherto known as *Nesionixalus thomensis* (Bocage, 1886), is endemic to the island of São Tomé (Fig. 1A); a second, recently elevated species, *N. mollerii* (Bedriaga 1892), is a smaller treefrog (Fig. 1B) present and widespread on both São Tomé and Príncipe. *Nesionixalus thomensis* was originally described as a member of the genus *Hyperolius* by Bocage (1886), the type material, five specimens from Roça Saudade (ca. 800 m), Rio Quiza (probably Rio Quija in SW part of the island; exact locality unknown), and Ile São Tomé was housed in the Museu Bocage in Lisbon. There the series was re-examined in the mid 1970s by Perret, who placed the species in a new genus, *Nesionixalus*, based on large snout-vent length (males: 30–35 mm; females: 42–47 mm), shape of digital tips (oval, broader than long), dorsal skin of males covered by fine spinosities (smooth in females), absence of vocal sac in males (m. interhyoideus undifferentiated), absence of buccal vocal sac openings in males, and large size but small number of eggs (Perret 1976). In 1978, the Museu Bocage was destroyed by fire and all herpetological material was lost (E.G. Crespo, *pers. commun.*).

In the course of his phylogenetic analysis of the Hyperoliidae which included 63 species of 15 genera (including *Semnodactylus* as *Kassina wealei*), Drewes (1984) located what appeared to be the only four museum specimens of *N. thomensis* still in existence, a male and female in London (BM 1951.1.1.91 and 98.3.30.39) and a pair in Vienna (NHMW 3695–6). The male specimens



Figure 1A–B. (A) *Nesionixalus* (= *Hyperolius*) *thomensis* ♀; CAS 218934, São Tomé Id: Macambrara. Photo by. D. Lin. (B) *Nesionixalus* (= *Hyperolius*) *mollerii* ♂; CAS 219203-07, Príncipe Id: Baía das Agulhas. Photo by R.C. Drewes.



exhibited vocal sacs consistent with Drewes' character 21, state 1 (e.g. sac simple; fibers of m. interhyoideus parallel) and buccal vocal sac openings consistent with character 20, state 2 (anterior slits). The four specimens were x-rayed but no additional character states were observed to support *Nesionixalus* as a separate genus within the context of Drewes' largely myo-skeletal data set, and he returned *Nesionixalus thomensis* to the synonymy of *Hyperolius thomensis* Bocage.

Four years later, Perret (1988) resurrected the genus *Nesionixalus*; he re-examined the Vienna material and while conceding the presence of the vocal sac and vocal sac openings as observed by Drewes (1984), he reiterated large snout-vent length, male integumental spinosities, transversely enlarged toe pads, and large size but small number of eggs (which he considered indicative of a specialized reproductive niche) as diagnostic. He added that the testes were large in size, the gular gland narrow and not conspicuous, and terminal phalanx obtuse or weakly notched ("*status 2 de Drewes, non hyperolien*"). He did not indicate which terminal phalanx nor how this latter observation was made. In the same work, Perret (1988) described three additional genera to accommodate Cameroonian species formerly accepted as members of the genus *Hyperolius* Rapp 1842: *Alexeroon* to include *Hyperolius obstetricans* Ahl, 1931, *Arlequinus* for *H. krebsi* Mertens, 1938, and *Chlorolius* for *H. koehleri* Mertens, 1940.

In 1992, Loumont reported on the results of field work undertaken in July 1988 and January 1990 on São Tomé and Príncipe; she revised the known amphibian fauna of both islands and provided the first chromosome data and advertisement calls for the endemic anurans. She recognized three hyperoliid tree frogs: *Leptopelis palmatus* (Peters 1868) known only from Príncipe; *Nesionixalus thomensis* (Bocage, 1886), endemic to São Tomé, and *Hyperolius molleri* Bedriaga, 1892, a green, moderate-sized treefrog which is numerous, widespread and endemic to both islands. Loumont (1992:51) placed *H. molleri* in the genus *Nesionixalus* along with *N. thomensis*, citing Perret's 1988 diagnostic characters. She also listed a number of character states in *N. molleri* that were more similar to typical *Hyperolius* than to *N. thomensis*. Loumont evidently collected no tissue samples and did not deal with anuran larvae — the tadpoles of the anuran endemics remain undescribed. In the same year, Loumont joined Schätti in a publication on the herpetofauna of São Tomé Island (Schätti and Loumont 1992).

In his additions and corrections to Frost's (1985) *Amphibian Species of the World*, Duellman (1993) recognized the genus *Nesionixalus* (*N. thomensis* and *N. molleri*) as well as the genera *Alexeroon*, *Arlequinus* and *Chlorolius* of Perret. Schiøtz (1999) included these taxa in his book on African treefrogs as well. In his generic description Schiøtz (1999, p.309) reiterates Perret's absence of vocal sac and vocal sac openings character states as diagnostic of the genus in spite of Drewes' (1984) demonstration of their presence in *Nesionixalus thomensis*, and Perret's (1988) subsequent acknowledgment that such is the case. Following his treatment of *N. thomensis*, *Nesionixalus molleri* is described as with a large gular sac (Schiøtz 1999:311).

To date, none of the species of *Nesionixalus*, *Alexeroon*, *Arlequinus* or *Chlorolius* has been tested or confirmed in a published molecular and/or morphological phylogenetic analysis.

## MATERIALS AND METHODS

Five species of *Hyperolius* and the two species of *Nesionixalus* (*N. thomensis* and *N. molleri* from both São Tomé and Príncipe) were used as the in-group in an initial analysis. *Leptopelis palmatus* was designated as the outgroup based on results from previous studies indicating that *Leptopelis* is at least basal to all other hyperoliid genera (Liem 1970; Drewes 1984; Channing 1989; Richards and Moore 1996; Emerson et al. 2000; Vences et al. 2003).

An approximately 2 kb sequence that includes part of the 12S and 16S ribosomal genes and



the t-RNA for valine was amplified and sequenced with the primers and protocols in Wilkinson et al. (1996) and Wilkinson (1997). All sequences produced for this study were deposited in GenBank (see Appendix, Table 1 for a list of sequences, their sources, and accession numbers).

The sequences were aligned following the procedure of Kjer (1993) using a putative secondary structure for *Rana catesbeiana* as a standard (Nagae 1988). Because of insertion and deletion events in variable regions, those bases considered to have ambiguous alignments were removed from the analyses.

We performed a maximum unweighted parsimony analysis using an exhaustive search. We also performed a bootstrap analysis (Felsenstein 1985) under maximum parsimony with 1000 replicates using the branch-and-bound search, and calculated Bremer's decay indices (Bremer 1994) to evaluate the amount of support for the resulting clades. The decay index analysis was facilitated by the program Autodecay (Eriksson 1998).

We performed a second analysis on approximately 500 b of only the 16S ribosomal gene in which, in addition to the species used in the first analysis, included DNA sequences retrieved from GenBank and Richards and Moore (1996) for two species each from the genera *Afrixalus*, *Heterixalus*, *Kassina*, the species *Tachycinemis seychellensis*, two more species and one more sub-species of the genus *Hyperolius*, and one more species from the genus *Leptopelis* (see Appendix, Table 1). Because of the additional taxa in this analysis, we used a heuristic search with 100 random stepwise additions followed by TBR branch swapping. We also performed a bootstrap analysis under maximum parsimony with 1000 replicates using the heuristic search with 10 random stepwise additions followed by TBR branch swapping and calculated Bremer's decay indices on this second data set. Museum symbolic codes used herein follow Leviton et al. (1985).

## RESULTS AND DISCUSSION

The first parsimony analysis resulted in one cladogram of 1167 steps with a consistency index (excluding uninformative characters) of 0.691, a retention index of 0.662, and a  $g_i$  statistics (Huelsenbeck and Hillis 1993) of -0.648 for the distribution of all possible trees in the exhaustive search. The second analysis resulted in four most parsimonious cladograms of 865 steps long with a consistency index (excluding uninformative characters) of 0.494 and a retention index of 0.613.

In both analyses *Nesionixalus thomensis* and *N. mollerii* formed a well-supported clade nested within the genus *Hyperolius*, with *H. cinnamomeoventris* as the sister taxon to the *Nesionixalus* clade (Figs. 2

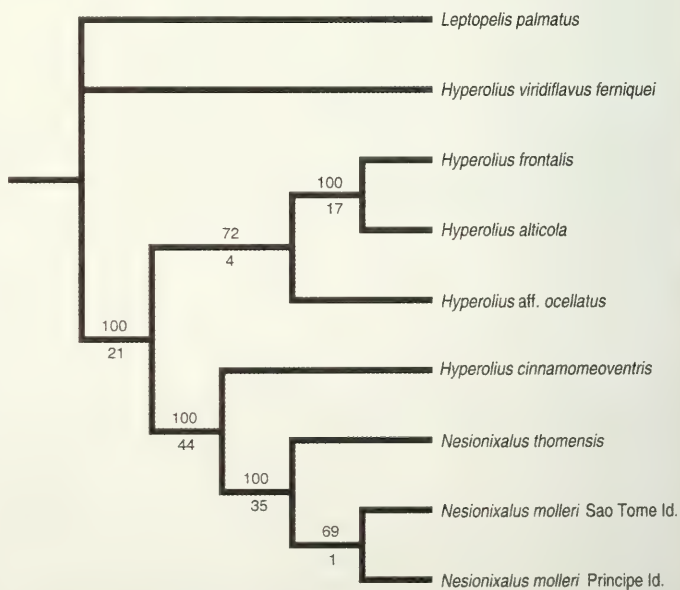


FIGURE 2. The most parsimonious cladogram resulting from an exhaustive search in a maximum parsimony analysis on approximately 2000 bases for five of the species of *Hyperolius* and two species of *Nesionixalus* in Table 1. Numbers above branches represent bootstrap support for the respective clade, while numbers below branches are decay indices.

and 3). In the second analysis, the genus *Hyperolius* formed a well-supported clade separate from all other genera in the analysis except *Nesionixalus* (Fig. 3). Also, *N. mollerii* (CAS 218848) from São Tomé formed a clade with *N. thomensis* instead of *N. mollerii* (CAS 219125) from Príncipe in two of the four most parsimonious cladograms, indicating that the reduced number of characters in this analysis could not separate *N. mollerii* from *N. thomensis*.

Our molecular results indicate two possible conclusions: either (1) *Nesionixalus* is not a valid genus (Drewes 1984), and both *N. thomensis* and *N. mollerii* are members of the genus *Hyperolius*, or (2) the species of *Nesionixalus* are a clade deserving of generic recognition, and their inclusion in the genus *Hyperolius* as currently recognized renders the latter paraphyletic.

In light of the results of the analyses above, we reexamined the characters used by Perret (1976, 1988) to define the genus *Nesionixalus*. We relied heavily on an unpublished M.A. dissertation by L.G. Wilson (2000). This work is important to a discussion of the genus *Hyperolius* for at least three reasons: (1) it is the first attempt at a phylogenetic analysis of the genus (Wieczorek et al. [2001] focused on a subset — the *H. viridiflavus* complex), (2) it includes the largest sample size (31) of *Hyperolius* species studied to date (fifty-one morphological characters were employed, and outgroup species included four of the genus *Afraxalus*, three of the Malagasy *Heterixalus*, and *Cryptothylax greshoffi*); and (3) it is the first cladistic analysis that includes three out of four of Perret's (1988) new genera, *Alexteroon*, *Chlorolius* and *Nesionixalus*. Specimens of *Arlequinus* have been unavailable for study thus far.

### Perret's Diagnostic Characters

Most of the characters used by Perret (1976, 1988) to define *Nesionixalus thomensis* are equivocal with the exception of the transverse oval shape of the finger and toe tips:

#### Size

Snout-vent lengths in the lost type series were given as 30.0 and 35.0 mm for the two adult

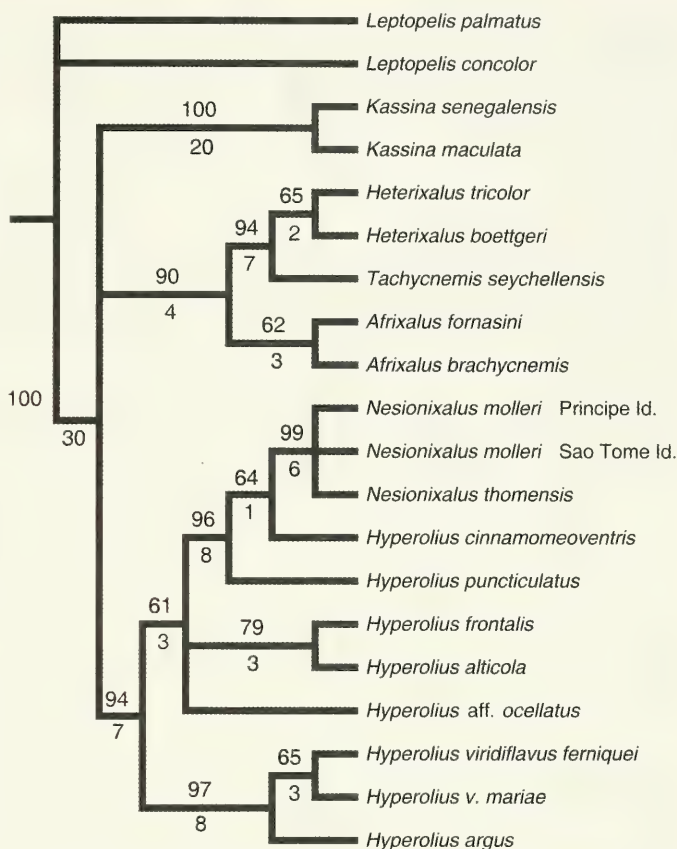


FIGURE 3. Strict consensus of four most parsimonious cladograms resulting from an heuristic search in a maximum parsimony analysis on approximately 500 bases for all species used in the analysis (Table 1). Numbers above and below branches are as in Fig. 2.

males, and 42.0 and 47.0 mm for the females; the fifth specimen of the series was evidently a juvenile at 18.0 mm (Perret, 1976). The 18 specimens in Loumont's (1992) collection were of snout-vent lengths 27.0–35.0 mm in males and 36.0–41.0 mm in females. CAS material includes two females at 47.5 and 49.2 mm and 11 adult males ranging from 35.4–41.1 mm; one male, likely subadult, of 31.0 mm was collected as a singleton (see Appendix, Table 2). Snout-vent lengths of *Nesionixalus thomensis* females do indeed exceed published records for members of the genus *Hyperolius*, but the females of a number of African mainland species attain or exceed 40.0 mm snout-vent lengths, including *Hyperolius torrentis*, *H. balfouri*, *H. sankuruensis*, *H. major* and *H. horstocki* with *H. bobirensis* of Ghana attaining snout-vent lengths of 47.0 mm (Schiotz 1999). The overall large size of *N. thomensis* may be attributed to the phenomenon of island gigantism, especially in light of the fact that there are many taxa endemic to São Tomé and/or Príncipe that exhibit the same phenomenon. For instance, the distantly related hyperoliid frog (*sensu* Drewes 1984), *Leptopelis palmatus*, endemic to the tiny island of Príncipe is the largest member of that genus and the largest African treefrog, with females reaching 110 mm snout-vent length. Another frog endemic to São Tomé, the ranine *Ptychadena newtoni* is the largest member of its genus (Loumont 1999). The gekkonid lizard, *Hemidactylus greeffii*, endemic to both islands, is the largest African species in the genus (Loveridge 1947) and the giant sunbird of São Tomé, *Dreptes thomensis*, is substantially larger than all other species in the Afro-Asian family Nectariniidae (Cheke et al. 2001). Among the angiosperms endemic to São Tomé is the giant, 2-m tall, *Begonia baccata*, a paleoendemic considered to be at least 3 million years old (Plana et al. 2004).

### ***Dorsal epidermal asperities***

Males of both *Nesionixalus thomensis* and *N. mollerii* (*sensu* Loumont, 1992) possess fine asperities (“*spinosités cornées*” of Perret 1988) which are relatively evenly spaced on dorsally exposed surfaces of the body. These structures are visible with little or no magnification; some, but not all of these asperities are black in *Nesionixalus* and the dorsal skin of females of both species lack them. This character is not unique to the island species; it is also shared by a number of mainland species of *Hyperolius*. Males of *H. spinigularis* have dorsal asperities, although these are not always pigmented (Schiotz 1975; 1999). All males in a large series of *H. alticola* (see Appendix, Table 2) from southwestern Uganda exhibit uniformly distributed spinosities (non-pigmented) which are absent in the females. Wilson (2000) coded the character state of dorsal spinules of *N. thomensis* and *N. mollerii* as the same in *Hyperolius bobirensis*, *H. endjami*, *H. laurenti*, *H. spinigularis*, *H. sylvaticus*, *H. tannerorum*, and *H. viridigulosus*, as well as in *Chlorolius koehleri* and *Alexteroon obstetricans*.

### ***Gular gland***

Perret (1988) described the gular gland of *N. thomensis* as narrow (“*mince*”), not obvious (“*peu apparente*”) and not very projecting [posteriorly?] (“*ne faint pas saillie*”). Wilson (2000) coded states of three characters of the male gular gland: size (four states based upon percent of gular area covered by the gland), thickness (four states based on gland thickness relative to that of surrounding, non-gland gular skin) and overlapping or free margins of the gland. The latter character, modified from Liem (1970), is a measurement of how much of the lateral and posterior borders of the gland cover distinct folds of distensible skin of the vocal pouch (Drewes 1984). The male gular glands of *N. thomensis* and *N. mollerii* occupy one-half or less of the total gular area, a character state shared by *Hyperolius laurenti*, *H. montanus*, *H. occidentalis*, *H. sylvaticus* and *Alexteroon obstetricans*; the thickness of the glands is the same as that of the glands of 24 of the



31 species of *Hyperolius* examined by Wilson (2000), and the extent of the glands free margins is the same as in *Hyperolius guttulatus*, *H. lamottei*, *H. laurenti*, *H. montanus*, *H. ocellatus* and *H. v. viridiflavus*.

### **Terminal Phalanx**

In the second description, Perret (1988) describes the terminal phalanx of *N. thomensis* as obtuse or weakly notched, as in Drewes (1984) state 2 [of character 14] and thus “*non hyperolien*.” Perret does not indicate which terminal phalanx nor the method of preparation, but this description is in error. All terminal phalanges in our cleared and stained material of both taxa are slender, and peniform with basal constriction, consistent with Drewes character 14, state 1, found in nine of the 12 species of *Hyperolius* he examined (Drewes, 1984, Fig. 10C; *H. balfouri* — not coded, *H. argus* and *H. phantasticus* had claw-shaped terminal phalanges — 14(0)). This character is of doubtful intergeneric utility as Wilson (2000) found three states of this character among species of *Hyperolius*. The condition of the terminal phalanges of both *N. thomensis* and *N. moller*i (MHNG specimens utilized by Loumont) was comparable to that in 22 of the 31 *Hyperolius* species cited in her study.

### **Size of testes**

Perret (1976, 1988) was impressed with the large size of the testes of the two males in the type series of *N. thomensis* (7 and 8 mm) and presented these data as a defining character in both the original and second description. Loumont (1992) reiterated this trait, noting that testes of *H. moller*i were also large (to 6.7 mm) and suggested this character together with the dorsal asperities justified placement of *H. moller*i in *Nesionixalus* Perret. In both descriptions, Perret (1976, 1988) added large size of eggs and small clutch size as further distinguishing *N. thomensis*. Wilson (2000) examined male testis size in *Hyperolius* and relatives and coded four states of this character based on testis length expressed as a percentage of total snout-vent length. *Nesionixalus thomensis* and *N. moller*i grouped with the eastern *Hyperolius tuberilinguis* at 19–21% of SVL and *H. bobirensis* and *H. montanus* had even larger testes at 25% and 34% SVL, respectively. All remaining *Hyperolius* fell within the 6–17% SVL range. Obviously the validity of this character depends upon the male frogs being at the peak of reproductive activity with testes fully enlarged; the fact that male *Hyperolius* are almost always located and collected while sexually active, together with Wilson's large sample size of males of 31 species of *Hyperolius*, suggest that these observations are reasonably accurate and that the testis size in *Nesionixalus* does not serve to differentiate the genus from *Hyperolius*.

### **Eggs and clutch size**

Comparative data regarding size of eggs and clutches among hyperoliid species are scarce. Members of the genus *Hyperolius* are generally described as having small eggs (0.8–1.5 mm) which in a few species are deposited in water or typically on vegetation above the water surface in clutches of 100 to 500 (Channing, 2001). Perret (1976) found 25 large (2.0–2.5 mm) presumably ovarian eggs in each of two of the three females in type series of *N. thomensis*; in erecting the genus he suggested that the small number and large size of the eggs might indicate a specialized reproductive mode “*un cycle biologique particulier*.” Loumont (1992) added new data for *H. thomensis* (50 to 60 ovarian [?] eggs of less than 0.5 mm diameter in two females) and *H. moller*i (70+ mature eggs per clutch, 1.5 mm diameter). However, Fahr (1993) presented a figure of an *H. moller*i egg mass, which included at least 110 eggs. Egg and clutch size are of questionable taxonomic value

for hyperoliid treefrogs; there are almost no data available on the former except perhaps scattered references in the experimental literature and relative to the number of species recognized, data are very sparse for the latter. In his comprehensive book, Schiøtz (1999) treated 85 species and species groups within the genus *Hyperolius* but was able to provide clutch size data for only 14 of them. Of these, five are known to deposit fewer than 50 eggs per clutch: *H. frontalis*, *H. mitchelli*, *H. mosaicus*, *H. pusillus* and *H. semidiscus*. Channing (2001) added clutch size data for four additional species including *H. pickersgilli* with 50 eggs.

### *Finger and toe tips*

The size and nature of expanded digital finger and toe tips was examined by Liem (1970); Drewes (1984) did not employ the character in his hyperoliid work. With respect to this character, Channing (1989) re-coded and used Liem's data on rhacophorids only. All of our specimens of *Nesionixalus thomensis* exhibit toe tips that are as previously described: enlarged, oval and wider in the horizontal plane than they are long — consistent with Liem's character 33, state 4 which he found common in a number of rhacophorid genera but not in any hyperoliid species. As Perret correctly observed (1976), the condition of *N. thomensis* digital expansions is very similar to that in *Acanthixalus spinosus* (see Appendix, Table 2), a West African hyperoliid not examined by Liem (1970). In addition, nearly identically-shaped digital tips are found in *Kassina maculifer* (*K. parkeri* of Scortecci 1932; Drewes 1984, 1985; Tandy and Drewes 1985; Appendix, Table 2 herein) of the arid Somali Horn. On the other hand, the expanded digital tips of all of our *N. mollerii* from both São Tomé and Príncipe Islands are disc-shaped, consistent with Liem's (1970) character 33, state 2, which he found in all *Hyperolius* and the majority of other hyperoliid genera he examined.

We did not make a broad survey of hyperoliid digital pads and concede that there are no species of *Hyperolius* known with digital tips similar to those of *N. thomensis*. However, this single character state is not sufficient to support recognition of a distinct genus; moreover, this state is not shared by the purported congener, *N. mollerii*. Other than toe pad shape and body size, all of the morphological characteristics used by Perret (1976, 1988) to define *Nesionixalus* and Loumont (1992) to subsequently reassign *H. mollerii* are shared by other species of *Hyperolius* or attributable to island effects. This coupled with the results of our molecular analysis indicate that the genus *Nesionixalus* Perret is not a lineage separable from *Hyperolius* and that *N. thomensis* and *N. mollerii* should be relegated to the synonymies of *Hyperolius thomensis* Bocage, 1886 and *Hyperolius mollerii* Bedriaga, 1892 respectively.

In all molecular studies to date, *Hyperolius* has been shown to be monophyletic with respect to other hyperoliid genera; however, sample sizes have been extremely limited (Richards and Moore 1996, three species; Emerson et al. 2000, three species; Wieczorek 1999, 14 species and 16 subspecies of the *H. viridiflavus* complex, but with *Afraxalus* as lone outgroup; Vences et al. 2003, six species). Similarly, all morphology-based phylogenetic studies support the monophyly of *Hyperolius* (Liem 1970, 14 *Hyperolius* species examined; Drewes 1984, 12 examined; Channing 1989, data from Drewes, *op. cit.* and Liem, *op. cit.*) and widely-cited, regional works have assumed it (e.g., Schiøtz 1967, 1975, 1999; Rödel 1996; Channing 2001). *Hyperolius* species can be extremely difficult to determine, especially after preservation; however, the genus has, until the recent descriptions of *Nesionixalus*, *Chlorolius*, *Arlequinus* and *Alexteroon* (Perret 1988; Amiet 2000) been rather easy to discern by initial determination of pupil shape (Drewes 1984:45–46). For instance, if the specimen in hand has horizontally-oval pupils (Fig. 4 B), is obviously arboreal with expanded digital tips (as opposed to *Chrysobatrachus*, which is terrestrial [Laurent, 1964]) and has a single gular gland in males (as opposed to *Acanthixalus*, in which gular glands are paired), it is a member of the genus *Hyperolius*.



At this time, we offer no taxonomic judgments on the validity of Perret's (1988) *Alexteroon*, *Chlorolius* and *Arlequinus*. We lack sequence data for these taxa, and morphological work suggesting the first two be returned to the genus *Hyperolius* is unpublished (Wilson 2000). The morphological definitions for *Alexteroon* and *Chlorolius* do not seem to include any synapomorphies that would serve to distinguish them unequivocally from *Hyperolius*, and in all cladograms presented by Wilson (2000), *Alexteroon*, *Chlorolius* and *Nesionixalus* nested within *Hyperolius* regardless of outgroup (*Afrixalus*, *Cryptothylax*). Diagnostic morphological character states used in the past (Liem 1970; Drewes 1984) would suggest that *Arlequinus* is most likely to have a separate evolutionary history from *Hyperolius*. *Arlequinus* shares the quadratic pupil shape with *Acanthixalus*, *Afrixalus*, *Heterixalus*, *Opisthophylax* and *Cryptothylax* within the Hyperoliidae (Fig. 4).

Monophyly in the genus *Hyperolius* has been either assumed by researchers or demonstrated (either morphologically or molecularly) on the basis of very small sample sizes relative to the number of currently recognized species. We contend that to make taxonomic decisions on member taxa in the absence of robust knowledge of relationships within the largest hyperoliid genus runs the risk of adding to an already confused situation. A modern revision of the genus *Hyperolius* based on both molecular and morphological data is a daunting but long overdue task. We do recognize that *H. malleri* and *H. thomensis* is a molecularly highly supported clade (as shown in Figs. 2 and 3). Moreover, both species share a chromosome number of  $2n = 26$  (Loumont 1992; Schätti and Loumont 1992; Fahr 1993), a condition rare among known *Hyperolius* species but not unique (Morescalchi 1968). However, to designate this clade a genus separate of *Hyperolius* would render *Hyperolius* paraphyletic, a result not supported by morphological analysis in this study. An intriguing



FIGURE 4. Pupil shapes within the Hyperoliidae. Liem (1970) and Drewes (1984) both recognized three states of pupil-shape among hyperoliid frogs, but both combined two of these shapes, the vertical ellipse and rhomboidal/quadrangular, into a single character state; Channing (1989) followed suit, utilizing the same data. Schiotz (1999:43) provided a key that attempts to clarify pupil-shape in both living and preserved specimens: "1a. Pupil horizontal, square or (after preservation) round", and "2b. Pupil vertically elliptical or rhomboidal." We feel that these treatments mask states which are probably not homologous. Here we present the range of hyperoliid pupil shapes based on photographs of living specimens.

A. vertical (vertical ellipse). *Kassina maculata* (CAS 184054; Photo by J. Vindum); B. horizontal (horizontal oval, round). *Hyperolius parkeri* (CAS 154572-72; Photo by J. Vindum); C. rhomboidal (quadrangular, square). *Cryptothylax greshoffii* (MHNG specimen; Photo by J.-L. Perret).

\*To our knowledge, members of these genera have never been photographed in life.



ing result of this study is the fact that this clade is more closely related to *H. cinnamomeoventris* than any other member of the genus studied; in fact, the support for this relationship is higher than within the *molleri/thomensis* clade itself (a Bremer's decay index of 44 as opposed to 35; Fig. 2), and to our *Hyperolius* aff. *ocellatus* sample from Bioko, the northern-most member of the island chain, which might be expected due to geographic proximity. *Hyperolius cinnamomeoventris*, usually readily identifiable, is among the most widespread member of the genus and one of the few species that inhabits both savannah and forest (Schjötz 1999). Such questions as the possible common ancestry of *H. cinnamomeoventris* and the island endemics can only be determined by a much more broadly representative sample of *Hyperolius* and other hyperoliid genera. So far, GenBank has sequence data for only 15 identified species of *Hyperolius* — along with 26 subspecies of the *H. viridiflavus* complex and four unidentified entities. Not counting *Nesionixalus*, *Arlequinus*, *Alexeroon* and *Chlorolius*, this represents about 12% of the species currently recognized in *Hyperolius* that are distributed throughout sub-Saharan Africa. There are undoubtedly tissues in museums that have not yet been sequenced, or sequences not yet entered into GenBank. At CAS, we have unsequenced tissues and vouchers for six such species and with the increase in fieldwork during the past decade especially in West Africa, there are no doubt many more at other institutions.

#### ACKNOWLEDGMENTS

We are grateful to Christina Richards of Wayne State University for loan of samples, Robert Jachens of USGS, Palo Alto, California for reviewing portions of the introduction and Lindsay G. Wilson for use of some of her data. The California Academy of Sciences Gulf of Guinea Expedition owes its success to the assistance of Ned Seligman, Director of STePUP, São Tomé, Angus Gascoigne of Voice of America, São Tomé, and Quintino Quade and our other field companions on both islands. We received necessary permits and much cooperation from Dr. Theresa D'Espiney, then-Director of ECOFAC and through the kind offices of the Hon. Maria das Neves Batista de Sousa, then-Minister of the Economy of the Republic of São Tomé and Príncipe. Additional thanks go to all of the members of the CAS expedition: Ricka Stoelting, Jens Vindum (Herpetology), Tomio Iwamoto (Ichthyology), Norman Penny, Charles Griswold, Joel Ledford (Entomology), Sarah Spaulding (Invertebrate Zoology), Douglas Long (Mammalogy), Dong Lin (Photography) and Fabio Penny (Education). The Expedition was funded by the Curators Research Fund and the G. Lindsay Field Research Fund, California Academy of Sciences and generous contributions to CAS Department of Herpetology by the late Richard A. Dumke, the late Malcolm and Jeanne Miller, David L. Jameson, and Emily Date. Early reviewers include R. Altig, and L.G. Wilson.

This paper represents contribution no. 35 of the Center for Biodiversity Research and Information of the California Academy of Sciences.

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APPENDIX

TABLE 1. Sources for DNA sequences used in this study.

Species	Source	GenBank Accession Number
<i>Afrixalus brachynemesis</i>	Richards and Moore (1996)	
<i>Afrixalus fornasinii</i>	GenBank	AFU22071
<i>Heterixalus boettgeri</i>	GenBank	HBU24672
<i>Heterixalus tricolor</i>	Richards and Moore (1996)	
<i>Hyperolius argus</i>	Richards and Moore (1996)	
<i>Hyperolius alticola</i>	CAS 207322	AY603984
<i>Hyperolius cinnamomeoventris</i>	CAS 202493	AY603985
<i>Hyperolius frontalis</i>	CAS 201986	AY603986
<i>Hyperolius aff. ocellatus</i>	CAS 207321	AY603988
<i>Hyperolius puncticulatus</i>	Richards and Moore (1996)	
<i>Hyperolius viridiflavus ferniquei</i>	CAS 191296	AY603987
<i>Hyperolius v. mariae</i>	GenBank	HVU22064
<i>Kassina maculata</i>	GenBank	KMU22072
<i>Kassina senegalensis</i>	Richards and Moore (1996)	
<i>Nesionixalus mollerii</i>	CAS 219125	AY603990
<i>Nesionixalus mollerii</i>	CAS 218848	AY603989
<i>Nesionixalus thomensis</i>	CAS 218925	AY603991
<i>Leptopeltis concolor</i>	GenBank	LCU22079
<i>Leptopeltis palmatus</i>	CAS 219177	AY603992
<i>Tachycinemesis seychellensis</i>	GenBank	TSU22080

TABLE 2. Preserved specimens examined.

Species	Museum Number	Locality
<i>Acanthixalus spinosus</i>	CAS 153799–800	Cameroon: Sangmelima, Foulassi, Ngam
<i>Hyperolius alticola</i>	CAS 180449–481	Uganda: Rukungiri Dist: Bwindi Impenetrable NP: Munyaga Rv.
<i>Nesionixalus</i> (= <i>Hyperolius</i> ) <i>thomensis</i>	CAS 218925–937; 219404	São Tomé e Príncipe: São Tomé Id: Macambrara.
<i>Kassina maculifer</i>	CAS 140351; 140353–354; 140356–361	Kenya: Wajir Dist: Wajir

## A New Species of *Dendrodoris* (Mollusca: Nudibranchia: Dendrodorididae) from the Pacific Coast of North America

David W. Behrens<sup>1,3</sup> and Ángel Valdés<sup>2,3</sup>

<sup>1</sup>Department of Invertebrate Zoology, California Academy of Sciences  
875 Howard Street, San Francisco, California 94103; <sup>2</sup>Natural History Museum of  
Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007

A new species of the genus *Dendrodoris*, *D. azineae*, is described based on a specimen collected from La Jolla Canyon, San Diego County, and photographs of animals from Sycamore Banks, Malibu and Carmel Bay, California. *Dendrodoris azineae* is characterized externally by its unique color, dissimilar to any described species worldwide, having purple gills and rhinophores. Internally, *D. azineae* differs from other eastern Pacific species in the size of the prostate and bursa copulatrix, and shape and size of the ampulla and the genital atrium. Thus far *D. azineae* is only known from southern to central California.

The status of species assigned to the family Dendrodorididae along the eastern Pacific coast has changed several times in recent years. Behrens (1991) reported seven nominal species — three yellow species: *Doriopsilla albopunctata* (Cooper, 1863), *Dendrodoris fulva* (MacFarland, 1905), and *Dendrodoris* sp. 1; one red to black species: *Dendrodoris krebsii* (Mörch, 1863); and three grayish pale or white species: *Dendrodoris nigromaculata*, *Dendrodoris* sp. 2, and *Dendrodoris* sp. 3. Later, Valdés and Behrens (1998) added *Doriopsilla spaldingi* Valdés and Behrens, 1998, to this fauna. One additional eastern Pacific dendrodoridid species, *Doriopsilla janaina* Marcus and Marcus, 1967, is found to the south within the Panamic Province (Marcus and Marcus 1967). Gosliner, Schaefer, and Millen (1999) described *Dendrodoris* sp. 1 as a new species, *Doriopsilla gemela* Gosliner et al., 1999, and at the same time regarded *D. fulva* as a junior synonym of *D. albopunctata*. Behrens (2004) noted the name change of *D. krebsii* on the Pacific coast of the Americas to *Dendrodoris fumata* (Rüppell and Leuckart, 1830), after Valdés et al. (1996) reported that the specimens from the Caribbean and Eastern Pacific were distinct. *Dendrodoris* sp. 3 remains undescribed. The present paper deals with recently collected material of *Dendrodoris* sp. 2.

The first known collection of *Dendrodoris* sp. 2 was made in 1977 in a benthic trawl sample taken by Dr. Rim Fay and Robert Henderson of the then Pacific Biomarine Laboratories, of Venice, California. The collectors noted that it was distinct from all other porostomes on this coast. Periodic trawls in the same area over the next several years failed to produce any additional specimens. This specimen has subsequently been lost. On 12 July 2000, Clinton Bauder photographed the species in about 54 m, in Carmel Bay, California (Rudman 2000; Behrens 2004). Bauder and his team of deepwater technical divers have searched for another specimen ever since with no success. Additionally, there have been several sightings of this species from 45–54 m, respectively in La

<sup>3</sup> Research Associate, Department of Invertebrate Zoology, California Academy of Sciences.

Jolla Canyon, San Diego, California by George Spalding III (Behrens 2004), but specimens were not collected.

The present paper describes this species based on the La Jolla specimen, which has been deposited in the type collections of the Natural History Museum of Los Angeles County.

### SPECIES DESCRIPTION

#### *Dendrodoris azineae* Behrens and Valdés, sp. nov.

(Figs. 1–3)

White Porostome Behrens, 1980:100–101

*Dendrodoris* sp. 2 Behrens, 1991:72

*Dendrodoris* sp. 3 Rudman, 2000:<http://www.seaslugforum.net/dendsp3.htm>

*Dendrodoris* sp. 2 Behrens, 2004:43

**TYPE MATERIAL.** — Holotype: LACM 3035, La Jolla Canyon, San Diego County, California, March 14, 2004, 54 m depth, one specimen 35 mm preserved length, collected by George Spalding III. The specimen is dissected.

**EXTERNAL MORPHOLOGY.** — Living animals reach up to 75 mm in length. The general color of the living animals varies from opaque white to a creamy-tan (Fig. 1). The margin of the notum is slightly ruffled and is edged with a white band. The clavus of the rhinophore is deep purple, below which the shaft has dense patches of the same purple on the posterior side. This gill is also purple.

The body is oval (Fig. 1), high, lacking spicules. The dorsum is smooth, with no tubercles. The posterior end of foot is translucent white. The rhinophores are perfoliate with 17 lamellae. The gill is composed of six bipinnate leaves which are somewhat separated from one another. The anus is central between the branchial leaves.

Ventrally there are no oral tentacles. The mouth is reduced to a pore.

**INTERNAL ANATOMY.** — The digestive system has an oval buccal bulb (Figs. 2A–B), with two strong retractor muscles attached. From the posterior end of the buccal bulb emerge the pharynx and a narrow duct that splits into two and connects to the ptyaline glands. The paired ptyaline glands are large and situated ventral to the anterior portion of the digestive system. The pharynx is long and connects directly to the esophagus through a narrow duct. The esophagus is also long and has two esophageal glands situated next to the connection of the pharynx. The esophagus widens progressively towards the posterior end and becomes wide and muscular proximally. The intestine is long and straight and bears a small, oval pyloric gland near its proximal end. The hermaphroditic gland is separated from the digestive gland.

The heart is large and connects to the blood gland through a conspicuous aorta. The blood



FIGURE 1. Living animals of *Dendrodoris azineae* sp. nov. (A) Holotype from La Jolla Canyon, California, 54 m depth (LACM 3035), photograph by Eric Hanauer. (B) Specimen from Carmel Bay, California, 54 m depth, 30 mm long, not collected, photograph by Clinton Bauder.



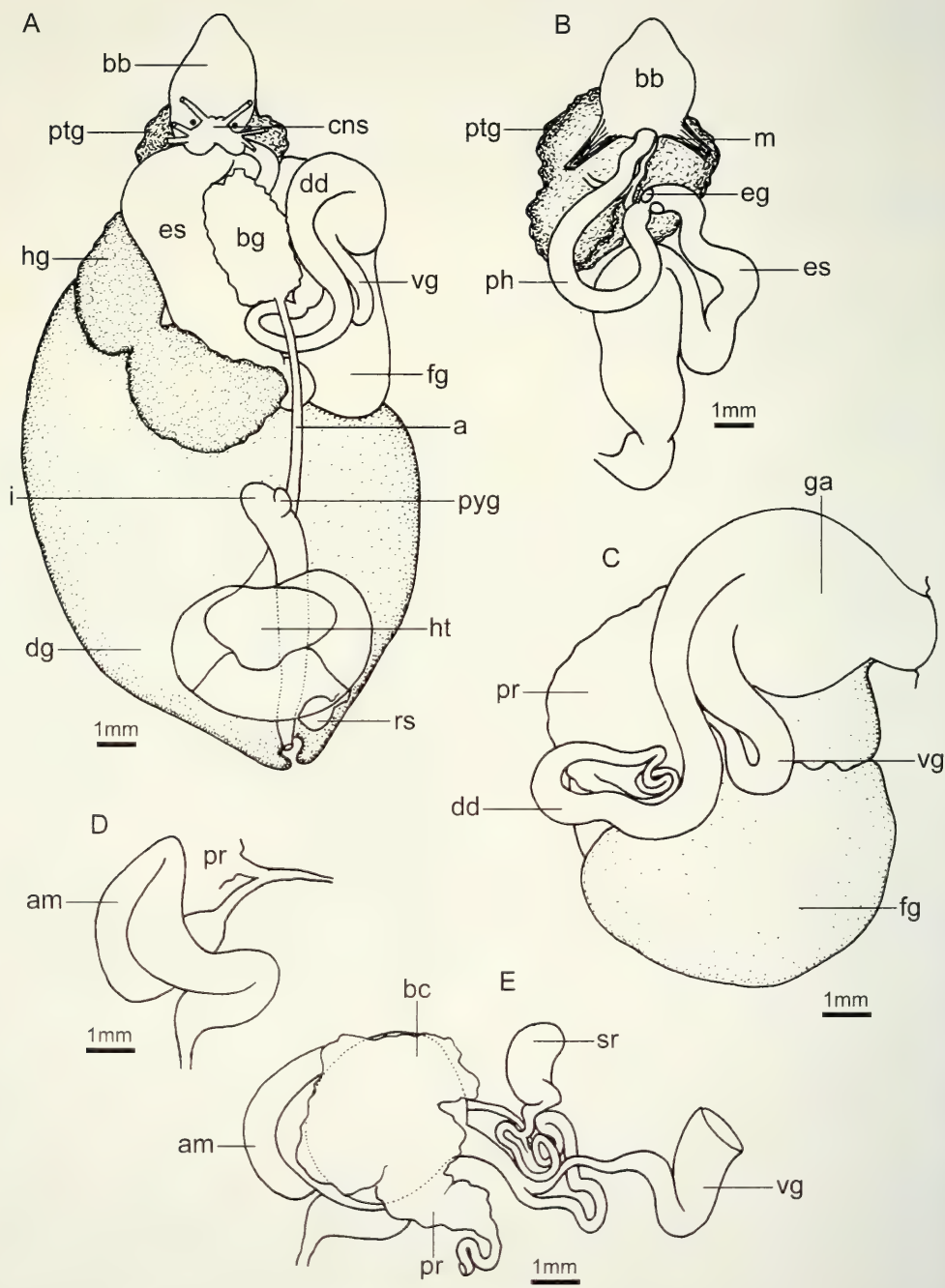


FIGURE 2. Anatomy of *Dendrodoris azineae* sp. nov. (LACM 3035). A. Dorsal view of anatomy. B. Anterior portion of the digestive system. C. General view of the reproductive system. D. Dissected view of ampulla and prostate. E. Dissected reproductive organs. Abbreviations: a = aorta, am = ampulla, bb = buccal bulb, bc = bursa compulatrix, bg = blood gland, cns = central nervous system, dg = digestive gland, dd = deferent duct, eg = esophageal gland, es = esophagus, fg = female gland, ga = genital atrium, hg = hermaphrodite gland, ht = heart, i = intestine, m = retractor muscle, ph = pharynx, pr = prostate, ptg = ptyaline gland, pyg = pyloric gland, rs = renal sac, sr = seminal receptacle, vg = vagina.

gland is situated posterior to the central nervous system and covers portions of the reproductive system. There is an oval renal sac situated on the right hand side of the heart and connected to the pericardium.

The reproductive system is triaualic (Figs. 2C–E). The ampulla is long and convoluted, and branches into a short oviduct and the prostate. The oviduct enters the female gland in the center of the mass. The prostate is flattened and short, covering most of the bursa copulatrix. The prostate connects with a narrow duct that expands into the long, wide and muscular deferent duct. The vaginal duct is very long and wide. Both the vaginal duct and the deferent duct open into a large, muscular genital atrium. The proximal end of the vaginal duct joins the rounded bursa copulatrix. From the bursa copulatrix leads another duct that branches into a short uterine duct and the pyriform seminal receptacle. The penis is very long and smooth, covered with several rows of penial hooks (Figs. 3A–B). The distal spines seem to include some longer, blunt spines.

**ETYMOLOGY.** — The name *azineae* was chosen at the request of George Spalding III of Solana Beach, California who collected the holotype. It is meant to honor his daughter Azine, who gives him the inspiration to continue his deep dives in search of new marine species in the La Jolla submarine canyon.

**DISTRIBUTION.** — Thus far the species is known from La Jolla Submarine Canyon (present study), Sycamore Banks, offshore of Malibu, California (Behrens 1980, 1991) and Carmel Bay, California (photographs by Clinton Bauder).

**NATURAL HISTORY.** — Little is known about the natural history of this species. It has not been observed with any sponge species. All specimens have been observed on sand or rock substrates. In his usual manner, Mr. Spalding recorded the water temperature at the time of collection of the holotype as 10.6°C, at the collection depth of 60 m. We have no information on the species' egg mass.

## DISCUSSION

This species is placed in the genus *Dendrodoris* Ehrenberg, 1831, because of the presence of the following combination of characters: dorsum lacking a network of spicules, anus located centrally between the branchial leaves, digestive system with two ptyaline glands, radula and jaws absent, and esophagus with a pair of esophageal glands. Valdés and Gosliner (1999) found these characters to be diagnostic for *Dendrodoris*, which is a monophyletic group.

A review of the literature shows that there are no other species with a similar external coloration to *Dendrodoris azineae*. The Atlantic species of the genus were reviewed by Valdés et al. (1996), who found considerable external variability within the nine taxa examined. However, none of the Atlantic species have a uniform white background color with purple rhinophores and branchial leaves. Brodie et al. (1997) examined the systematics of the tropical Indo-Pacific species *Dendrodoris nigra* (Stimpson, 1855) and *Dendrodoris fumata* (Rüppell and Leuckart, 1830). These authors also found great external variability in these two species, but none of the color forms are similar to *D. azineae*.

There are no other described species of the genus *Dendrodoris* along the coast of California. *Dendrodoris fumata* is the only other species of *Dendrodoris* described from the eastern Pacific. This tropical species is found within the Panamic Province, from México to the Galápagos Archipelago (Behrens 2004). Valdés et al. (1996) described the external morphology of eastern Pacific specimens of this species under the name *Dendrodoris nigra* (Stimpson, 1855). It differs from *Dendrodoris azineae* in several regards, including the presence of a uniformly colored (yellow, pink, gray, orange, red, or black) background (Brodie et al. 1997) and wider mantle margin with conspicuous striations. Brodie et al. (1997) described the anatomy of *D. fumata*, which has a

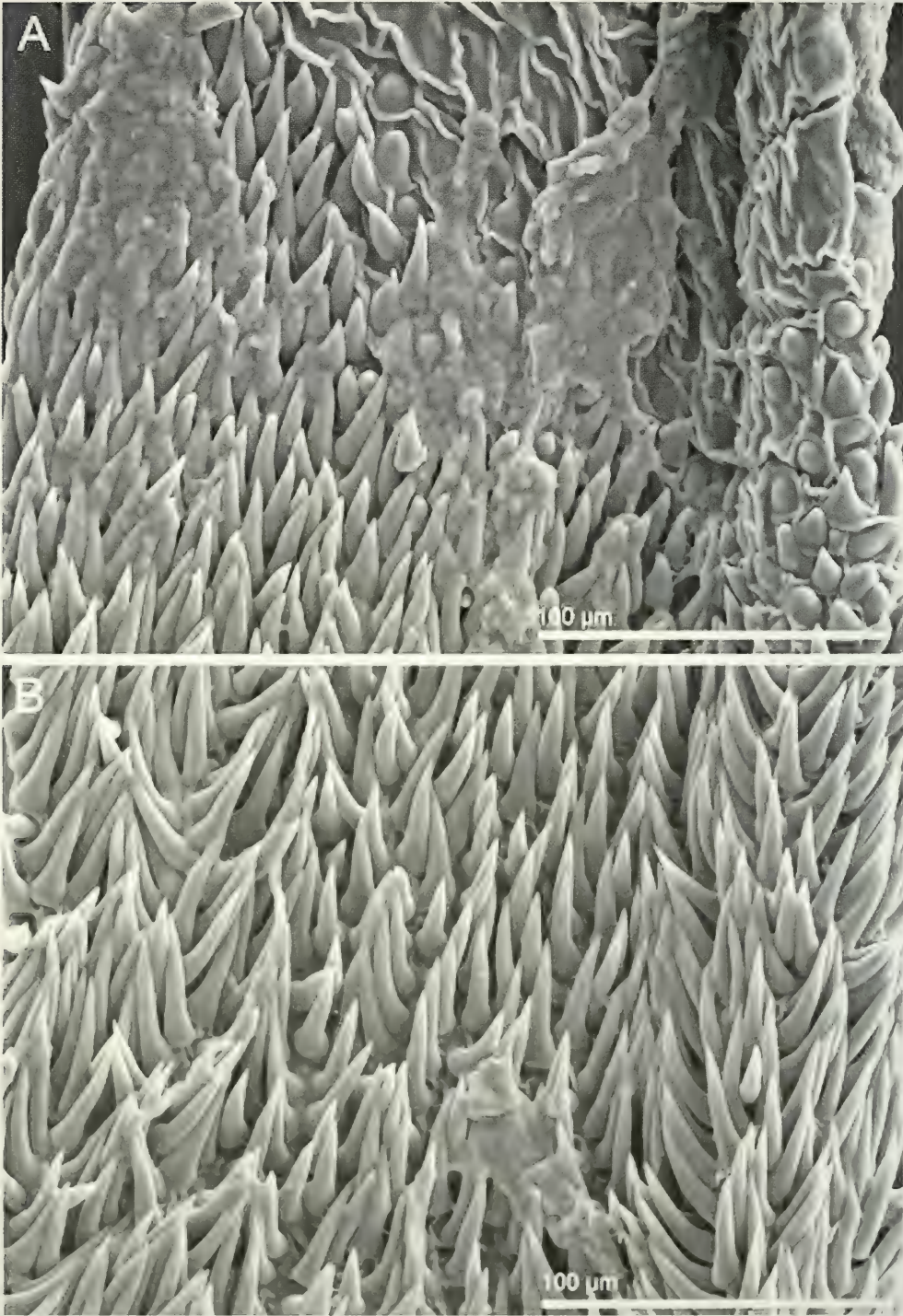


FIGURE 3. Scanning electron micrographs of the penial spines of the holotype of *Dendrodoris azineae* sp. nov. (LACM 3035). A. Distal portion of the penis, B Proximal portion of the penis.



prostate much smaller than that of *D. azineae* and the bursa copulatrix and seminal receptacle are about the same size, whereas in *D. azineae* the bursa copulatrix is much larger. Other differences include the shape and size of the ampulla, which is shorter and wider in *D. fumata*, and the genital atrium, which is much larger in *D. azineae*.

*Dendrodoris* sp. 3, *sensu* Behrens (1991), is also a white species, but it differs from *Dendrodoris azineae* by having large brown spots on the dorsum and white rhinophores and branchial leaves. This species remains undescribed.

#### ACKNOWLEDGMENTS

The authors would like to recognize the generous efforts of all of those who have spent many hours searching over the past 20-plus years for specimens of this new species: Clinton Bauder and his fellow members of the Bay Area Underwater Explorers, George Spalding III, Peter Brueggeman, Jim Lance, Rim Fay and Bob Henderson. Thanks also to Eric Hanauer and Clinton Bauder for permitting us to use their photographs for preparation of the color images.

This paper was supported by the National Science Foundation through the PEET grant DEB-9978155 *Phylogenetic systematics of dorid nudibranchs* to Terrence M. Gosliner and the junior author.

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## Systematics of *Okenia* from the Pacific Coast of North America (Nudibranchia: Goniodorididae) with Descriptions of Three New Species

Terrence M. Gosliner<sup>1</sup> and Hans W. Bertsch<sup>2</sup>

Department of Invertebrate Zoology and Geology, California Academy of Sciences,  
875 Howard Street, San Francisco, California 94103;

<sup>1</sup> E-mail: [tgosliner@calacademy.org](mailto:tgosliner@calacademy.org); <sup>2</sup> [hansmarvida@sbcglobal.net](mailto:hansmarvida@sbcglobal.net)

The systematics of the eastern Pacific species of *Okenia* are reviewed. The anatomy of *Okenia vancouverensis* (O'Donoghue, 1921) and *O. angelensis* Lance, 1966 is described more completely. Three new species of *Okenia* are described from the tropical eastern Pacific. *Okenia angelica* sp. nov. is characterized by its purplish body color with numerous elongate lateral papillae and short, rounded dorsal tubercles. It is known from Baja California to Jalisco, México. *Okenia cochimi* sp. nov. has a bright uniformly yellow body with numerous lateral appendages and a single medial appendage anterior to the gill. It is known from Cedros Island, the central Gulf of California and Bahía Banderas, México. *Okenia mexicorum* is white with brick red markings. It has short lateral appendages, and a mid-dorsal crest that terminates in a single elongate papilla. This species is known from the central Gulf of California to Bahía Banderas, México.

### RESUMEN

La posición sistemática de las especies de *Okenia* del Pacífico Este es revisada. La anatomía de *Okenia vancouverensis* (O'Donoghue, 1921), y *O. angelensis* Lance, 1966, es descrita detalladamente. Tres especies nuevas de *Okenia* son descritas del Océano Pacífico Este Tropical. *Okenia angelica* esp. nov. es caracterizada por tener un cuerpo violeta con papilas laterales largas y numerosas y tubérculos dorsales cortos y redondeados. Esta especie es conocida de Baja California hasta Jalisco, México. *Okenia cochimi* esp. nov. tiene un cuerpo amarillo brillante y uniforme, apéndices laterales numerosos y un apéndice medio situado en frente de la branquia. Esta especie es conocida de la Isla Cedros, la región central del Golfo de California y Bahía Banderas, México. *Okenia mexicorum* esp. nov. es blanca con áreas de color rojo teja. Esta especie tiene apéndices laterales cortos y una cresta media que termina en una papila larga. Esta especie es conocida de la región central del Golfo de California hasta Bahía Banderas, México.

Recently, the systematics of *Okenia* has been reviewed based on a preliminary phylogenetic analysis (Gosliner 2004). From this analysis came the conclusion that *Hopkinsia*, *Hopkinsiella* and *Sakishimaia* should be regarded as junior synonyms of *Okenia*. Four species of *Okenia* have been recorded from the Pacific coast of North America, *Okenia vancouverensis* (O'Donoghue, 1921); *O. rosacea* (MacFarland, 1905); *Okenia angelensis* Lance, 1966 and *Okenia plana* Baba, 1960. In this work, aspects of the anatomy of two northeastern Pacific taxa were presented. The radular teeth

and reproductive anatomy of *Okenia rosacea* (MacFarland, 1905) were described. The anatomy of Indo-Pacific and non-indigenous specimens of *Okenia plana* Baba, 1960, from the Philippines and San Francisco Bay was described. The description of the anatomy of these species will not be repeated here. O'Donoghue's (1921) description of *Okenia vancouverensis* included a description of the external morphology and the radula. In Lance's (1966) original description of *O. angelensis*, he described the external anatomy, the radular teeth and the shape of dermal spicules. The description of these species is amplified here. Expeditions to Baja California over the last twenty years have produced collections of two additional species of *Okenia*. More recent collections from the Pacific coast of México by Orso Angulo Campillo and Alicia Hermosillo have yielded specimens of a third undescribed species. The descriptions of these species are presented here.

All specimens examined here are housed in the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ).

## SPECIES DESCRIPTIONS

### Genus *Okenia* Menke, 1830

Type species: *Okenia elegans* (Leuckart, 1828), by monotypy.

#### *Okenia vancouverensis* (O'Donoghue, 1921)

(Figs. 1–2)

*Idalia vancouverensis* O'Donoghue, 1921:177, pl., fig. 22.

**MATERIAL EXAMINED.**—CASIZ 035222, one specimen, dissected, Rose Harbor, Queen Charlotte Islands, British Columbia, Canada, 4 July, 1913, Will F. Tompson.

**DISTRIBUTION.**—Known only from the Queen Charlotte Islands (present study), Vancouver Island, British Columbia, Canada to Puget Sound, Washington (Behrens 1991).

**NATURAL HISTORY.**—Found in about 15 meters of water on hard mud substrate.

**EXTERNAL MORPHOLOGY.**—The body is broad and ovoid (30 mm in length, in the preserved specimen) with nine to ten pairs of elongate, acutely pointed papillae situated along the notal margin and with an additional 24 similarly-shaped papillae on the remainder of the notum. The living animal is depicted by Behrens (1991) and Rudman (2003). The body is brownish with opaque white spots and an opaque white medial line along posterior portion of the foot. The rhinophores also contain patches of brown pigment. The rhinophores are elongate with 24 densely arranged lamellae. The gill consists of 12 bipinnate to tripinnate branches. Ventrally the foot is broad. The head (Fig. 1A) surrounding the mouth is broad and contains a pair of rounded oral lobes extending laterally. The reproductive opening is situated on the lateral side of the body, approximately one third of the length of the body posterior to the anterior margin.

**DIGESTIVE SYSTEM.**—The buccal mass (Fig. 1B) is thick and muscular with a an elongate buccal pump directed posteriorly. Numerous minute oral glands are present at the opening of the buccal mass into the mouth. The radular sac is elongate and extends ventrally and anteriorly from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A large, flat, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular polygonal plates. The cuticle expands as it enters the buccal pump. The radular formula is 32 X 1.1.0.1.1. in the single specimen examined (Fig. 2A). The inner lateral teeth (Fig. 2B) are wide basally with an elongate acutely pointed cusp. The masticatory margin of the inner lateral bears 7–9 triangular denticles that increase in size in



the direction of the outer margin. The outer laterals are large and hook-shaped (Fig. 2B) with a curved, acutely-pointed cusp.

**CENTRAL NERVOUS SYSTEM.**—The ganglia of the central nervous system are highly concentrated and surround the esophagus, at the posterior end of the buccal mass. The cerebral and pleural ganglia are entirely fused. A sessile eye is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure. Paired buccal ganglia are situated ventral to the esophagus.

**REPRODUCTIVE SYSTEM.**—(Fig. 1C) The preampullary duct is thin and elongate and expands into the relatively short, sausage-shaped ampulla. The ampulla divides into a short oviduct that enters the female gland mass and a more elongate vas deferens. The proximal portion of the vas deferens enters a large spherical

prostate that consists of numerous nodular bodies. From the prostate gland the ejaculatory duct emerges as a thin convoluted duct, which widens and forms several coils on top of the female gland mass. It then straightens and continues as an elongate duct that eventually widens slightly into the muscular penial bulb. The vagina is very wide at its exit adjacent to the penis, and consists of several folds. More distally it narrows and continues as a curved duct that again narrows and consists of a section that is folded and twisted together as convolutions. It then straightens again as it enters the base of the large, rounded bursa copulatrix. From the base of the bursa is a second duct that joins with the equally-sized, more pyriform receptaculum seminis. Near the base of the receptaculum, the uterine duct separates from the duct joining the receptaculum and bursa and enters the female gland mass. The female gland mass consists of three portions, the albumen, membrane and mucous glands. The mucous gland is the largest of the nidamental glands.

**DISCUSSION.**—*Okenia vancouverensis* is immediately identifiable by its broad body and brown color with opaque white markings. The present material agrees closely with that originally described by O'Donoghue (1921). O'Donoghue did not describe the anatomy of the reproductive system. *Okenia vancouverensis* appears to be unique among described *Okenia* species in having a discrete prostate gland rather than a prostate that merely represents an expansion of the deferent duct. The external anatomy of *O. vancouverensis* is similar to that described for *O. aspersa* (Alder & Hancock, 1845) and *O. leachi* (Alder & Hancock, 1854), both known from the northern Atlantic.

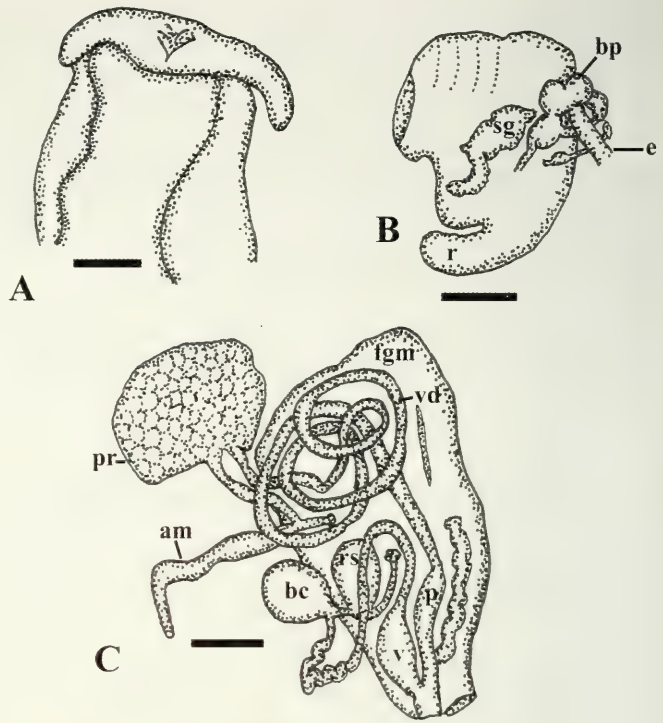


FIGURE 1. *Okenia vancouverensis* (O'Donoghue, 1921). A. Ventral view of head region, scale = 8.0 mm. B. Buccal mass, bp = buccal pump, e = esophagus, r = radular sac, sg = salivary gland, scale = 0.75 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 1.0 mm.

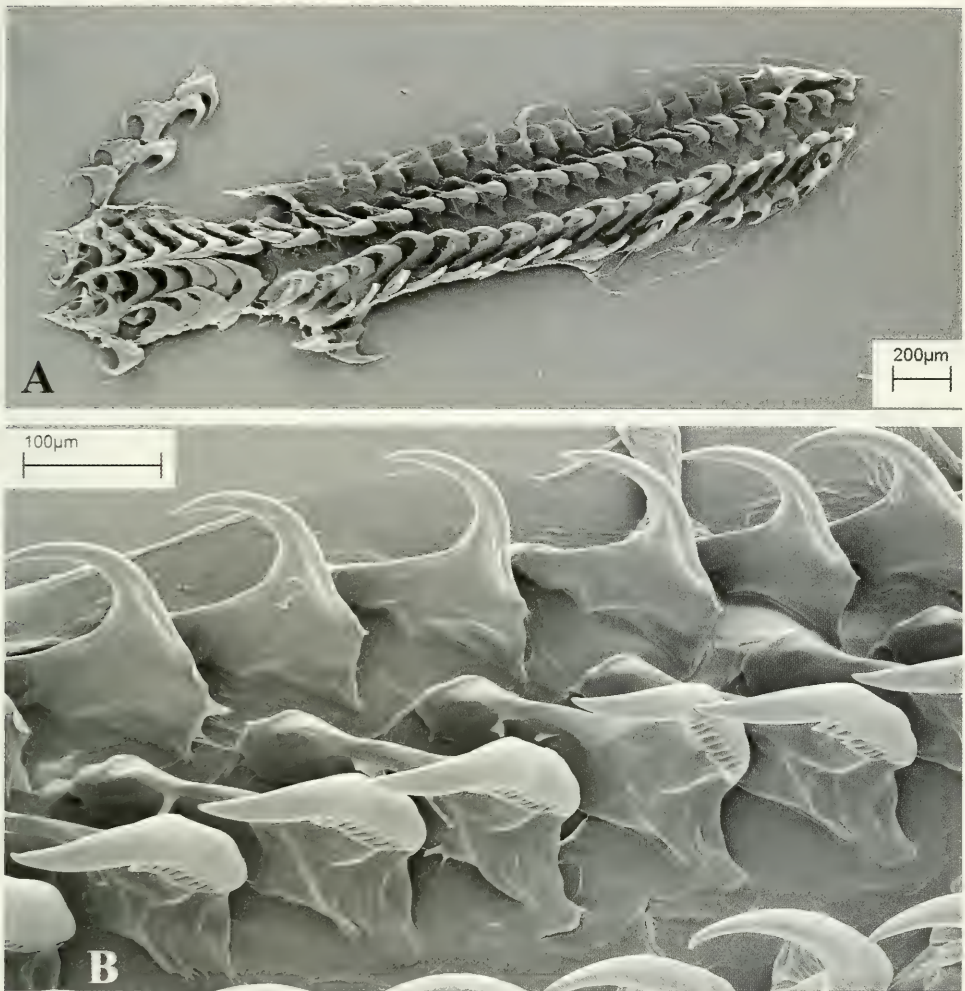


FIGURE 2. *Okenia vancouverensis* (O'Donoghue, 1921). Scanning electron micrographs of radular teeth. A. Entire radula. B. Inner and outer lateral teeth.

These two species, like *O. vancouverensis*, are also found on muddy substrate. *Okenia aspersa* differs from *O. vancouverensis* in having unevenly sized lateral appendages, with the anteriormost pair being the most elongate. *Okenia leachi* is similar to *O. vancouverensis* in having uniformly-sized lateral and notal papillae except the papillae are much longer in *O. leachi*. The radular teeth of *O. leachi* differ from those of *O. vancouverensis* in having far more denticles on the inner lateral teeth and in having a proportionately smaller outer lateral tooth with a shorter cusp (Thompson and Brown 1984, fig. 7h). The radular teeth of *O. aspersa* are very similar in shape and size to those of *O. vancouverensis* (Thompson and Brown 1984, fig. 7g). The inner lateral teeth of *O. aspersa* bear up to 17 denticles while those of *O. vancouverensis* have only 7–9 denticles.

*Okenia angelensis* Lance, 1966

(Figs. 3–4)

*Okenia angelensis* Lance, 1966:76, figs. 9–12.

**MATERIAL EXAMINED.**— CASIZ 072351, 4 specimens, one dissected, Morro Bay, California, May–June 1981, David Behrens. CASIZ 170047, 5 specimens, 2 dissected, Mission Bay, San Diego, California, on floating docks, 25 June 1987, Terrence M. Gosliner. CASIZ 070471, 10 specimens, 2 dissected, Texaco Marina, Morro Bay, California, 26 October, 1975, Gary McDonald.

**DISTRIBUTION.**— Known from San Francisco Bay to México and then disjunctly to southern Chile (Behrens, 1991, Muñoz et al., 1996).

**NATURAL HISTORY.**— Found from shallow embayments on floating docks or in the shallow subtidal zone.

**EXTERNAL MORPHOLOGY.**— The body is elongate (3–10 mm in length) with seven to eight pairs of elongate, rounded papillae situated along the notal margin and with an additional 8 papillae situated on the notum. The body is translucent yellowish white with numerous fine brownish spots scattered uniformly over the surface of the notum. The rhinophores are elongate with two to three well-spaced lamellae. The gill consists of five to seven unipinnate branches. The anterior margin of the head includes two elongate oral tentacles that extend anterolaterally.

**DIGESTIVE SYSTEM.**— The buccal mass (Fig. 3A) is thin and muscular with a rounded buccal pump directed dorsally. Numerous small, elongate, pyriform oral glands are present at the opening of the buccal mass into the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. No discrete polygonal plates were evident. The cuticle expands as it enters the buccal pump. The radular formula is 19 X 1.1.0.1.1 and 24 X 1.1.01.1 in two specimens examined. The inner lateral teeth (Fig. 4) are wide basally with an elongate acute bifid cusp. The masticatory margin of the inner lateral bears 15–19 triangular denticles that increase in size in the direction of the outer margin. The outer laterals are small and reduced with two short, acutely pointed cusps along the outer edge.

**REPRODUCTIVE SYSTEM.**— (Fig. 3B) The preampullary duct is thin and elongate and expands into the elongate, sausage-shaped ampulla. The ampulla divides into a short oviduct that enters the female gland mass and a more elongate vas deferens. The proximal portion of the vas

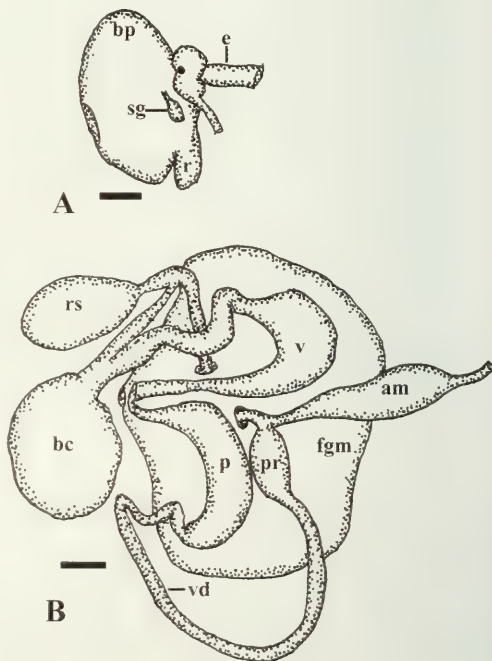


FIGURE 3. *Okenia angelensis* Lance, 1966. A. Buccal mass, bp = buccal pump, e = esophagus, r = radular sac, sg = salivary gland, scale = 0.15 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 0.17 mm.



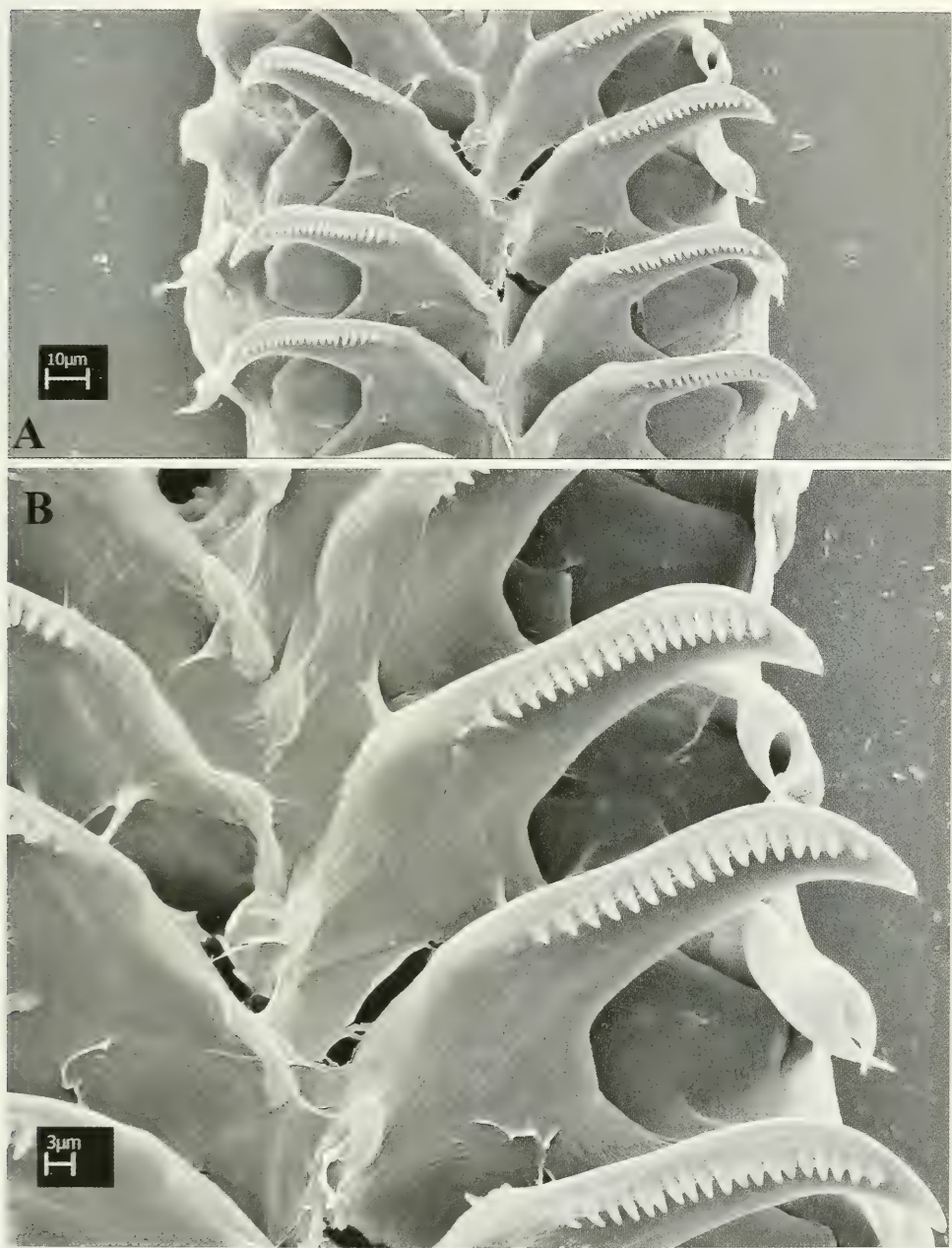


FIGURE 4. *Okenia angelensis* Lance, 1966. Scanning electron micrographs of radular teeth. A. Entire radular width. B. Inner and outer lateral teeth.

deferens is prostatic but very short. It narrows and continues as an elongate loop that eventually narrows slightly into the highly convoluted muscular, proximal ejaculatory portion. The penial bulb is wide and curved. The vagina is wide at its exit adjacent to the penis. More distally it narrow and continues as a thin duct that enters the base of the large, spherical bursa copulatrix. From the base of the bursa is a second duct that joins with the smaller, more pyriform receptaculum seminis. Near

the base of the receptaculum, the uterine duct separates from the duct joining the receptaculum and bursa and enters the female gland mass. The female gland mass consists of three portions, the albumen, membrane and mucous glands. The mucous gland is the largest of the nidamental glands.

**DISCUSSION.**— *Okenia angelensis* is immediately identifiable by its translucent yellowish white body color with minute brown spots. The present material agrees closely with that originally described by Lance (1966). Additional details of the anatomy including the morphology of the digestive and reproductive systems are added here.

***Okenia angelica* Gosliner and Bertsch, sp. nov.**

(Figs. 5A, 6–7)

**TYPE MATERIAL.**— **HOLOTYPE:** CASIZ 170088, 1 specimen, Punta Gringa, Bahía de los Ángeles, Baja California, México, Oct. 2, 1984, Terrence M. Gosliner. **PARATYPES:** CASIZ 166889, 1 specimen, dissected, Baja California, México, Feb. 18, 1999, Sandra Millen. CASIZ 170089, 1 specimen, San Carlos, Sonora, México, Dec. 1970. CASIZ 170090, 2 specimens, 1 dissected, Punta Gringa, Bahía de los Ángeles, Baja California, México, June 30, 1987, Terrence M. Gosliner. CASIZ 116929, 1 specimen, Isla Cedros, Pista, Baja California, México, April, 23, 1998, Hans Bertsch. CASIZ 170085, 1 specimen, Punta Gringa, Bahía de los Ángeles, Baja California, México, Sept. 20, 1985, Terrence M. Gosliner. CASIZ 170087, one specimen, Punta Gringa, Bahía de los Ángeles, Baja California, México, 6 October, 1984, Terrence M. Gosliner. CASIZ 170086, one specimen, Punta Gringa, Bahía de los Ángeles, Baja California, México, 24 October, 1986, Hans Bertsch. CASIZ 167395, 1 specimen, Mismaloya, Bahía de Banderas, Jalisco, México, 28 February 2003, Alicia Hermosillo.

**ETYMOLOGY.**— The specific name, *angelica*, comes from the fact that this species has an angelic appearance.

**DISTRIBUTION.**— This species is known only from Bahía de los Ángeles, Baja California to the Bahía de Banderas region near Puerta Vallarta, Jalisco, México (present study).

**NATURAL HISTORY.**— This species is found on small stones in 1–2 meters of water. It appears to be associated with bryozoans. The white egg mass is a thick cylindrical coil of approximately 1.25–1.5 whorls. This species has been documented over a decade from Bahía de los Ángeles where its presence is highly seasonal and variable (Tables 1–2).

**EXTERNAL MORPHOLOGY.**— The living animals (Fig. 5A) are small, 10–20 mm in length. The preserved specimens are 3–4 mm long. The body is moderately wide and ovoid and relatively high in lateral profile. There is a well-developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body color is deep purplish with an extensive opaque white patch on the center part of the notum. The white patch may also have areas of orange pigment. The margins of the notum, foot, bases of the rhinophores, lateral papillae, tubercles and gill are all covered with dark purple pigment. The apices of the lateral papillae and rhinophores are covered with light orange pigment. The tips of the gill branches are covered with dark brown. There is a lateral band of chocolate brown and irregular tubercles of the same color scattered over the notum over the opaque white. Seven to nine elongate and slightly curved papillae are scattered along either side of the notum. The posterior pair of papillae on either side share a common base. No mid-dorsal papillae are present on the notum, but rounded irregular tubercles are present. The gill consists of 5–10 unipinnate branches. The rhinophores are elongate with 16–18 congested lamellae. The anterior end of the broad foot (Fig. 6A) contains two elongate triangular velar lobes that are united medially. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head.



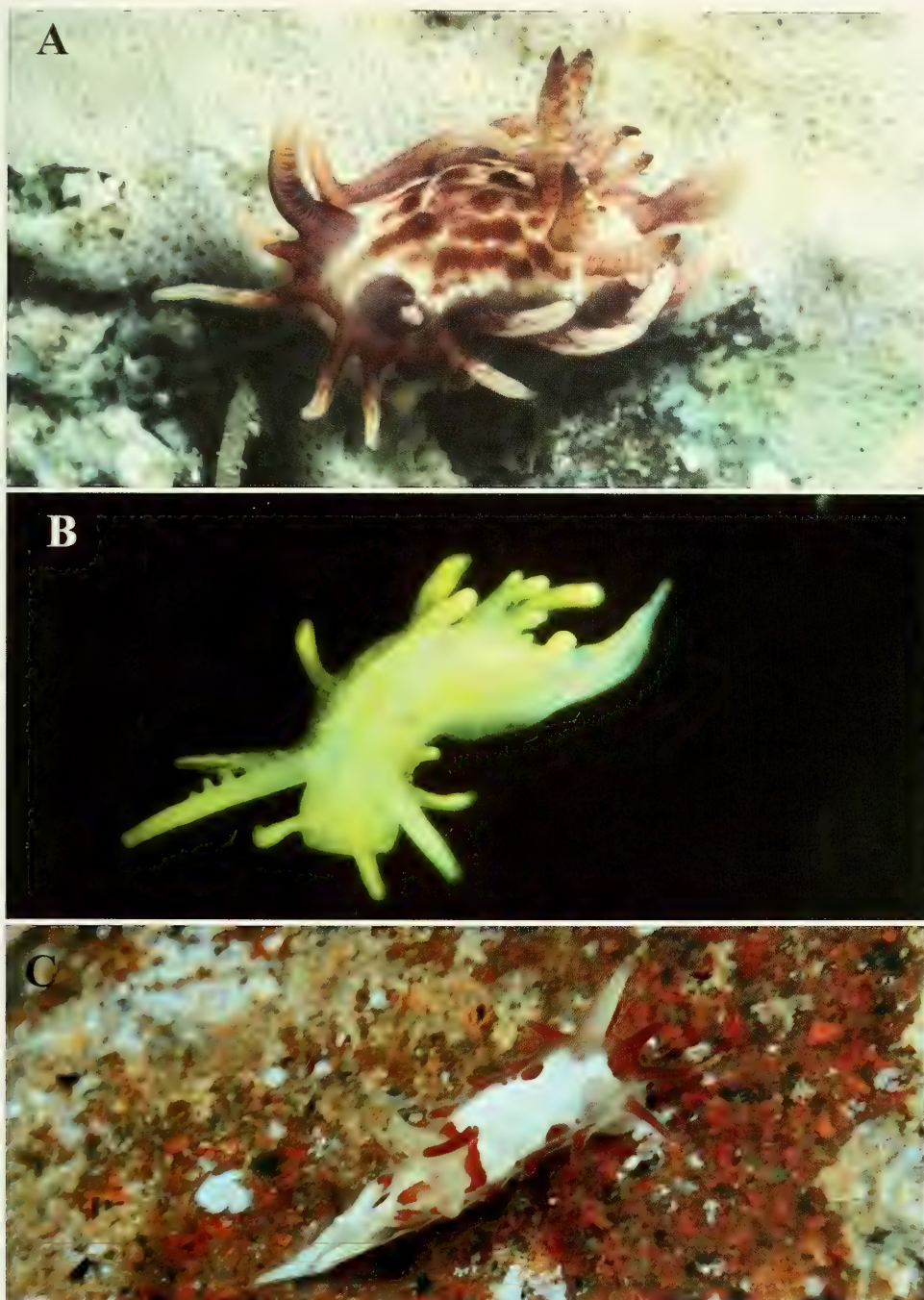


FIGURE 5. Living animals. A. *Okenia angelica* sp. nov., Punta Gringa, Bahía de los Ángeles, Baja California, México, photo by Terrence M. Gosliner. B. *Okenia cochimi* sp. nov., Las Ballenas, Espíritu Santo Island, Baja California Sur, México, photo by Terrence M. Gosliner. C. *Okenia mexicorum* sp. nov., Bahía de Banderas, Jalisco, México, photo by Alicia Hermosillo.



TABLE 1. Summary of annual observations of *Okenia angelica* at Bahía de los Ángeles during the 10 year period of 1992–2001. Columns indicate year, total hours of search time, number of animals seen, and density per hour.

Year	Hours	# Specimens	Density/hour
1992	27.52	2	.072
1993	23.57	8	.339
1994	42	25	.6
1995	30.3	5	.165
1996	24.8	1	.04
1997	36.55	1	.027
1998	13.7	4	.29
1999	18.15	7	.39
2000	15.7	1	.064
2001	18.05	13	.72

TABLE 2. Summary of monthly observations of *Okenia angelica* at Bahía de los Ángeles during the 10 year period of 1992–2001. Columns indicate totals for each month of hours searched, number of specimens, and density per hour.

Month	Hours	# Specimens	Density/hour
Jan	18.34	0	— (1 egg mass)
Feb	16.47	0	—
Mar	16.7	2	.12
Apr	11.27	0	—
May	17.1	1	.058
June	33	0	— (1 egg mass)
July	39.92	30	.75 (egg masses)
Aug	9.65	1	.1 (egg masses)
Sept	26.47	6	.23 (egg masses)
Oct	4.55	1	.22
Nov	34.35	22	.64 (egg masses)
Dec	17.08	3	.18

**DIGESTIVE SYSTEM.**— The buccal mass (Fig. 6B) is thick and muscular with a rounded buccal pump directed dorsally. There are 3–4 minute, simple pyriform oral glands on either side of the mouth. The radular sac is short and extends ventrally from the buccal mass. The cuticle expands as it enters the buccal pump. A labial cuticle surrounds the lips at the opening of the mouth. Discrete jaw elements are visible at the apex of the cuticle. The labial elements (Fig. 7A) have a broad quadrangular shape with 2–4 rounded apical lobes. The radular formula is 25 X 1.1.0.1.1. in one specimen examined. The inner lateral teeth (Fig. 7B) are broad basally with an elongate, acutely pointed cusp and 29–31 elongate fine, acutely pointed denticles along the elongate masticatory margin. The outer laterals are slightly smaller (Fig. 7B) with a quadrangular shape and rounded margin without a distinct cusp.

**REPRODUCTIVE SYSTEM.**— (Fig. 6C) The preampullary duct is short and thin and expands into sausage-shaped ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic

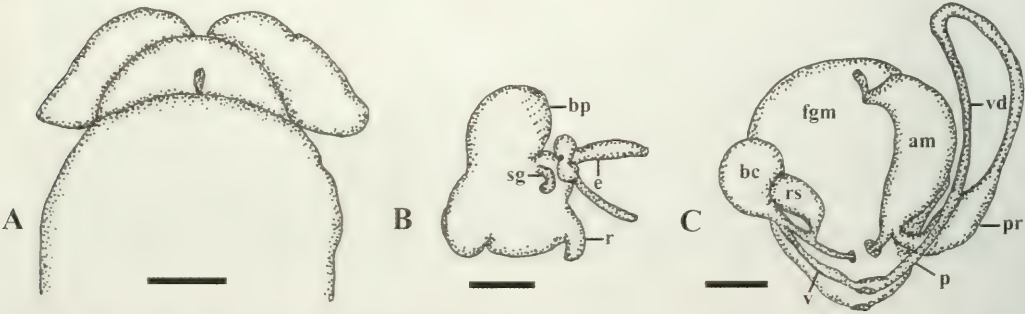


FIGURE 6. *Okenia angelica* sp. nov., A. ventral view of head, scale = 0.5 mm. B. Buccal mass, bp = buccal pump, e = esophagus, r = radula sac, sg = salivary gland, scale = 0.38 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 0.5 mm.

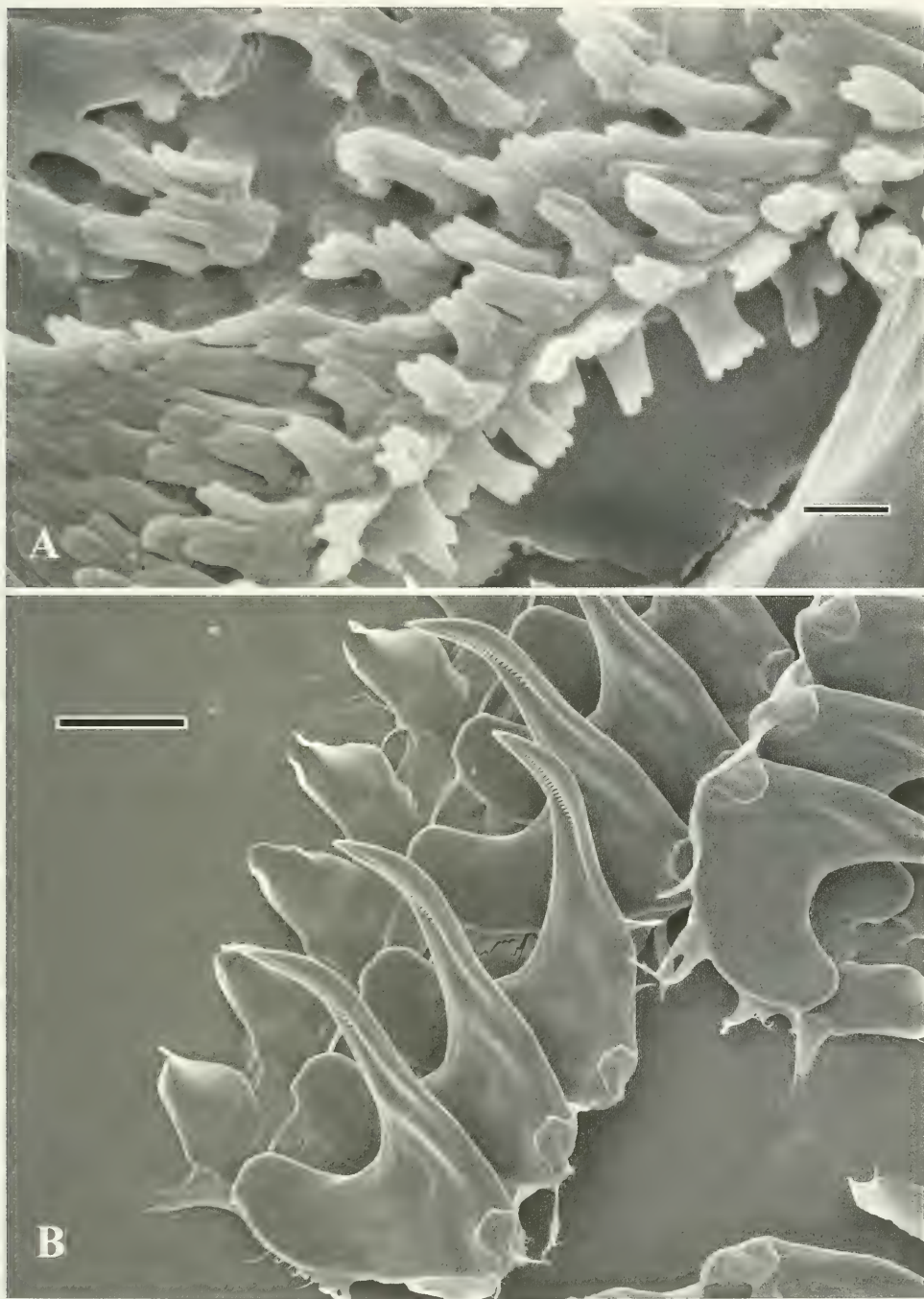


FIGURE 7. *Okenia angelica* sp. nov.. Scanning electron micrographs. A. Jaw rodlets, scale = 10  $\mu$ m. B. Radular teeth, scale = 40  $\mu$ m.

portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is short and wide. The distal end of the prostate narrows into a elongate, curved ejaculatory portion that terminates in a slightly wider penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is narrow and elongate and connects directly to the large, spherical bursa copulatrix. At the base of the bursa, the receptaculum duct emerges and joins the large, pyriform receptaculum seminis. The uterine duct emerges from near the base of the receptaculum and enters the female gland mass after paralleling the vagina for some distance.

**DISCUSSION.**— The only other described species of *Okenia*, besides *O. angelica*, that have bilobed, flat velar tentacles are *O. echinata* Baba, 1949 and *O. opuntia* Baba, 1960, both known only from Japan. All three species also have prominent jaw elements and similarly shaped radular teeth. Both of these species differ from *O. angelica* in having elongate papillae over the entire surface of the notum. *Okenia echinata* is orange or brown with minute opaque white spots. *Okenia opuntia* which also shares the character of having the posterior pair of notal appendages having a united base, is whitish with papillae that are yellow basally and white apically. *Okenia angelica* has 25 rows of radular teeth with 29–31 denticles on the inner lateral teeth. There are 40 rows of radular teeth with 30–35 denticles on the inner laterals of *O. opuntia* while in *O. echinata* there are 15 rows of radular teeth with 20–25 denticles on the inner laterals. Other details of the anatomy, including the reproductive morphology, were not described for the two Japanese species.

***Okenia cochimi* Gosliner and Bertsch, sp. nov.**

(Figs. 5B, 8–9)

**TYPE MATERIAL.**— HOLOTYPE: CASIZ 170091, one specimen, 13 m depth, Las Ballenas Espiritu Santo Island, Baja California Sur, 26 July, 1985, Terrence M. Gosliner. PARATYPES: CASIZ 170833, one specimen, 13 m depth, Las Ballenas Espiritu Santo Island, Baja California Sur, 26 July, 1985, Terrence M. Gosliner. CASIZ 170092, one specimen, dissected, Isla Cedros, Baja California, México, 29 December, 1985, Hans Bertsch.

**ETYMOLOGY.**— The specific epithet, *cochimi*, comes from the name for the Cochimí tribe of native Americans that inhabited central Baja California.

**DISTRIBUTION.**— This species is known only from the Isla Cedros on Pacific coast of Baja California, from Isla Ballena near La Paz in the Gulf of California south to Bahía Ballena near Puerto Vallarta, México (present study).

**NATURAL HISTORY.**— This species has been found in relatively shallow water of 10–15 meters depth, but has not been found in association with any prey species.

**EXTERNAL MORPHOLOGY.**— The living animals are small, 2–4 mm in length. The body is moderately elongate and relatively high. There is a well-developed, distinct notal border. The foot extends posteriorly and is devoid of papillae. The body color is uniformly lemon yellow. There are 5–8 pairs of elongate lateral papillae along the sides of the body. The two anteriormost papillae are situated in front of the rhinophores and are anteriorly directed. A single medial papilla is present mid-dorsally anterior to the gill. The gill consists of four unipinnate branches. The rhinophores are elongate with 5–6 congested lamellae. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head. The foot is narrow and is wider anteriorly. The oral region is rounded and lacks distinct tentacles (Fig. 8A).

**DIGESTIVE SYSTEM.**— The buccal mass is thick and muscular with a rounded buccal pump directed dorsally. Numerous, large, elongate, pyriform oral glands are present at the opening of the



buccal mass into the mouth. The radular sac is short and extends ventrally from the buccal mass. The esophagus is thin and elongate and inserts into the buccal mass immediately ventral to the buccal pump. A rounded, lobate salivary gland is present on either side of the buccal mass anterior to the junction of the esophagus with the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth. It contains irregular polygonal plates. The cuticle expands as it enters the buccal pump. The radular formula is 13 X 1.1.0.1.1. The inner lateral teeth (Fig. 9A–B) are wide basally with an elongate acute cusp. The masticatory margin of the inner lateral bears about 16–19 triangular denticles that increase in size in the direction of the outer margin. The outer laterals are small and reduced (Fig. 9A–B) and are triangular in shape with a short curved cusp at the apex.

**CENTRAL NERVOUS SYSTEM.**—The ganglia of the central nervous system are highly concentrated and surround the esophagus, at the posterior end of the buccal mass. The cerebral and pleural ganglia are largely fused. A sessile eye is present at the base of either cerebral ganglion. The pedal ganglia are smaller than the cerebropleural ganglia and are separated by a short commissure. Paired buccal ganglia are situated ventral to the esophagus.

**REPRODUCTIVE SYSTEM.**—(Fig. 8B) The preampullary duct is long and thin and expands into an ovoid ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of a single, folded portion. The distal end of the prostatic segment narrows into a short, straight ejaculatory portion that terminates near the base of the short, wide penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is narrow throughout its relatively short length. It connects directly to the irregularly shaped, elongated bursa copulatrix and the smaller, pyriform receptaculum seminis. Near the base of the receptaculum seminis, the uterine duct separates and enters the albumen gland.

**DISCUSSION.**—No other described species of *Okenia* has a uniformly colored yellow body. Several other species, including *O. angelensis* and *O. cupella* have a cream to yellowish color (present study; Valdés and Ortea 1995) but have scattered brownish markings, more widely separated rhinophoral lamella and a more elongate body. Several other species *Okenia* have lateral appendages with a single median dorsal papilla. In a study of the Indo-Pacific species (Gosliner 2004), these taxa were found in two primary clades, one that includes the species *O. lambat* Gosliner, 2004, *O. virginiae* Gosliner, 2004, and *O. kendi* Gosliner, 2004. These taxa are united in having a short vagina with the uterine duct emerging directly off the vagina rather than from the base of the receptaculum seminis. This differs from the elongate vagina of *O. cochimi*. These taxa also have small oral glands, unlike those found in *O. cochimi*. The second clade that includes species with a single mid-dorsal papilla is the one that includes *O. japonica* Baba, 1949; *O. pur-*

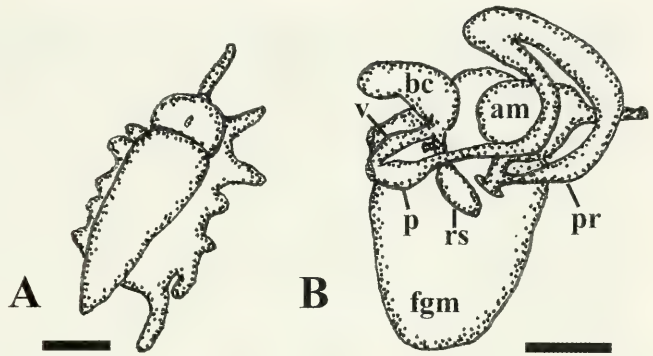


FIGURE 8. *Okenia cochimi* sp. nov., A. ventral view of head, scale = 0.2 mm. B. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, scale = 0.17 mm.

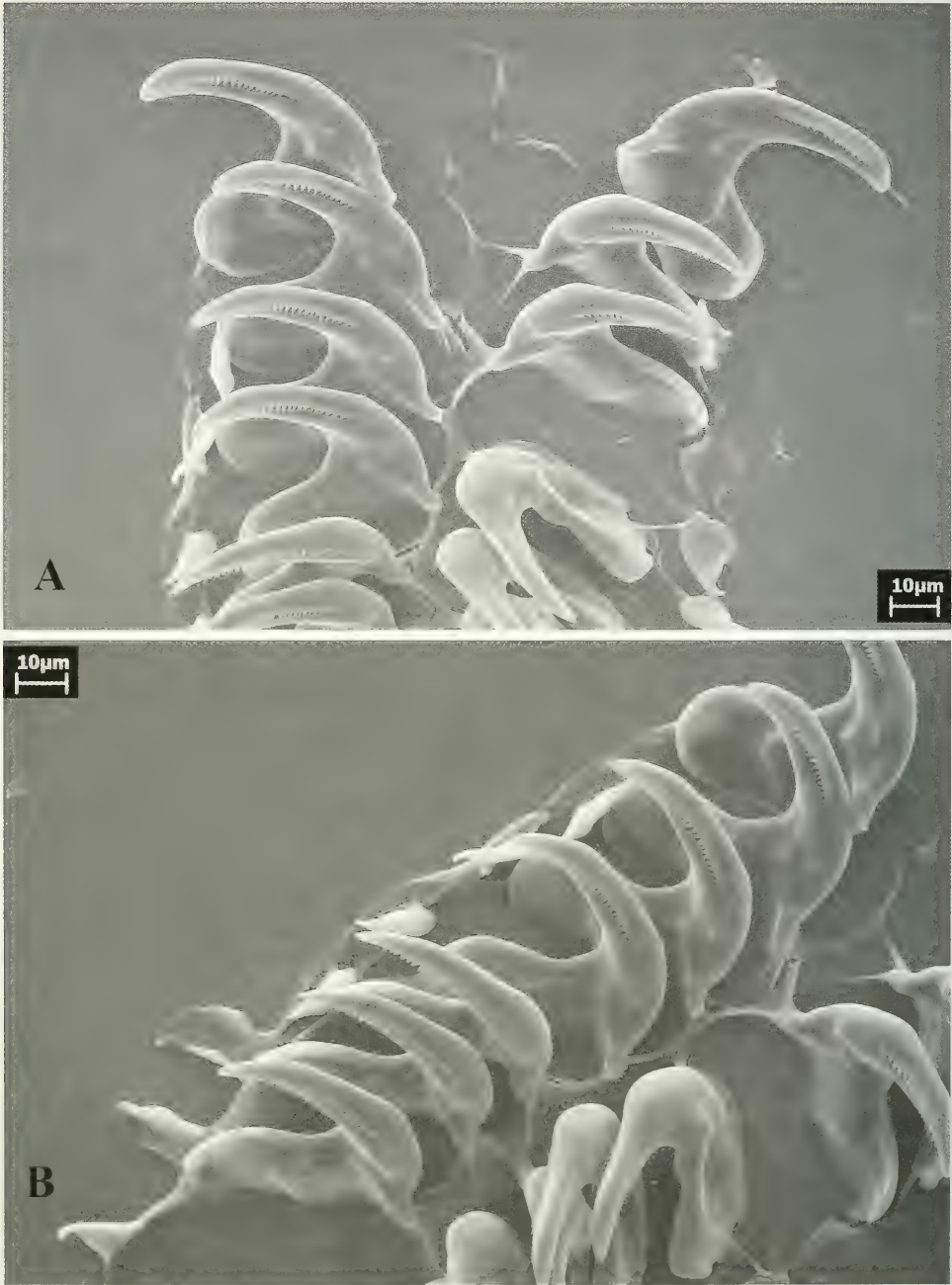


FIGURE 9. *Okenia cochimi* sp. nov. Scanning electron micrographs of radular teeth. A.Radular teeth. B. View of half row of radular teeth.

*pureolineata* Gosliner, 2004 and *O. liklik* Gosliner, 2004. Members of this group have a more elongate body shape and large oral glands, as in *O. cochimi*. All of these species are clearly distinct from *O. cochimi*. *Okenia japonica* is uniformly white with a light gray to opaque white dusting

over the entire body surface, while *O. cochimi* is yellow throughout the body. Both *O. purpureolineata* and *O. liklik* have a purple body color with darker purple lines in the case of *O. purpureolineata* or with brown and white markings in *O. liklik*. *Okenia cochimi* and *O. japonica* have a single elongate mid-dorsal papilla while *O. purpureolineata* has two elongate mid-dorsal papillae and in *O. liklik* the papilla has been modified to form a short sail-shaped ridge. The outer lateral teeth of *O. japonica* and *O. purpureolineata* are quadrangular while those of *O. cochimi* and *O. liklik* are triangular with an elongate, curved cusp.

***Okenia mexicorum* Gosliner and Bertsch, sp. nov.**

(Figs. 5C, 10–11)

**TYPE MATERIAL.**— **HOLOTYPE:** CASIZ 166888, one specimen, 20 m depth, Mismaloya, Bahía de Banderas, Jalisco, México, 28 February 2003, Alicia Hermosillo. **PARATYPES:** CASIZ 170044, 5 specimens, 2 dissected, 20 m depth, Mismaloya, Bahía de Banderas, Jalisco, México, 17 November 2003, Alicia Hermosillo. CASIZ 170043, 8 specimens, 20 m depth, Mismaloya, Bahía de Banderas, Jalisco, México, 22 November 2003, Alicia Hermosillo. CASIZ 167394, 1 specimen, 20 m depth, Majahuitas, Bahía de Banderas, Jalisco, México, 29 May 2003, Alicia Hermosillo. CASIZ 170045, 3 specimens, 1 dissected, 1 m depth, Ensenada de los Muertos, Baja California Sur, México, 25 October 2001, Orso Angulo Campillo.

**ETYMOLOGY.**— The specific name, *mexicorum*, honors our outstanding young Mexican colleagues, Alicia Hermosillo and Orso Angulo Campillo who have advanced greatly our understanding of the opisthobranch fauna of the tropical Americas.

**DISTRIBUTION.**— This species is known along the Mexican coast from Baja California Sur to Bahía de Banderas, Jalisco.

**NATURAL HISTORY.**— *Okenia mexicorum* has been found in relatively shallow water from 1–20 m depth. Specimens are found in the open on hard and soft substrate, but this species has not been found in association with prey species.

**EXTERNAL MORPHOLOGY.**— The living animals (Fig. 5C) are small, 5–8 mm in length. The preserved specimens are 2–3 mm. long. The body is moderately wide and ovoid and relatively high in lateral profile. There is a well-developed, distinct notal border. The foot extends posteriorly and is devoid of notal papillae. The body color is translucent white with an extensive opaque white patch on the center part of the notum that extends from the level of the rhinophores to the posterior end of the foot. External to this white patch are brick red pigmented areas that extend along the notal

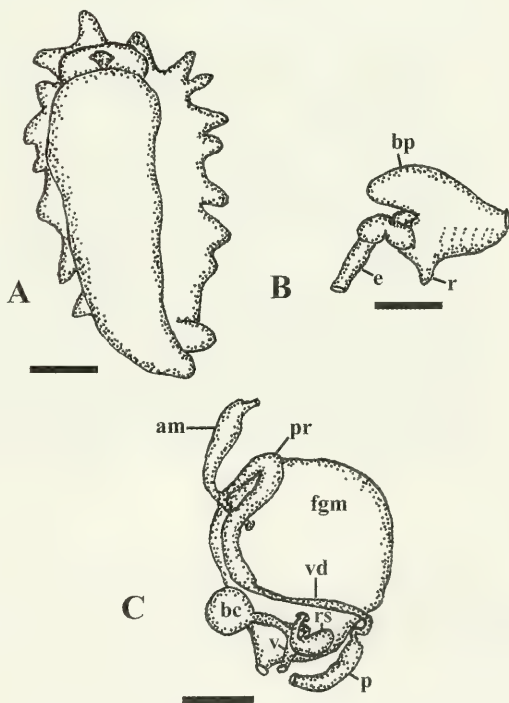


FIGURE 10. *Okenia mexicorum* sp. nov. A. ventral view of body, scale = 0.3 mm. B. Buccal mass, bp = buccal pump, e = esophagus, r = radula sac, scale = 0.2 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vas deferens, scale = 0.2 mm.





FIGURE 11. *Okenia mexicorum* sp. nov. Scanning electron micrograph of radular teeth. A. Inner and outer lateral teeth. B. Half-row of radular teeth.

margin and are also present on the eight to ten pairs of lateral papillae and on the single, elongate medial papilla located immediately anterior to the gill. This papilla is found at the posterior end of a long, elevated medial ridge. Red pigment patches are also found on the lateral sides of the body. Two pairs of these papillae are found anterior to the rhinophores while the remaining ones are posterior and extend to the level posterior to the gill. The posterior two papillae per side are much longer than the more anterior ones and do not share a common base. The rhinophores are uniformly white and have 7–9 simple lamellae. The apices of a few of the more posterior lateral papillae have opaque white or translucent white pigment. The gill consists of five to six unipinnate branches which bear mottled brick red pigment on their surfaces. The anterior end of the broad foot (Fig. 10A) is simply rounded without distinct oral tentacles. The genital aperture is situated on the right side of the body approximately a third of the length of the body posterior to the head.

**DIGESTIVE SYSTEM.**— The buccal mass (Fig. 10B) is thick and muscular with a rounded buccal pump directed dorsally. There are several small oral glands around the mouth. The radular sac is long and curved and extends ventrally from the buccal mass. A labial cuticle surrounds the lips at the opening of the mouth but no discrete jaw elements are visible. The cuticle expands as it enters the buccal pump. The radular formula is 15 X 1.1.0.1.1. in one specimen examined. The inner lateral teeth (Fig. 11A–B) are broad basally with a sharp curvature that places the thickened masticatory margin at a 90 degree angle relative to the basal portion. The masticatory portion has an acutely pointed cusp with 26–34 short, triangular acutely pointed denticles along its cutting edge. The outer laterals are significantly smaller and reduced (Fig. 11A–B) with a single curved, sharply pointed cusp.

**REPRODUCTIVE SYSTEM.**— (Fig. 10C) The preampullary duct is short and thin and expands into sausage-shaped ampulla. The ampulla divides into a short, narrow oviduct and the wider prostatic portion of the vas deferens. The oviduct enters the lobate female gland mass that consists of a small albumen gland, a lobed membrane gland and a larger, smooth mucous gland. These nidamental glands exit ventrally to the vagina and penis. The prostatic portion of the vas deferens is wide and consists of two folded segments. The distal end of the prostatic segment narrows into an elongate, curved ejaculatory portion that terminates in a long wider, curved penis. There is no distinct penial papilla. The vagina exits adjacent to the penis. It is narrow and moderately long and connects directly to the large, spherical bursa copulatrix. Near the base of the vagina, the receptaculum duct emerges and parallels the vagina for a short distance prior to joining the large, pyriform receptaculum seminis. The uterine duct emerges from near the base of the receptaculum and enters the female gland mass.

**DISCUSSION.**— No other species of *Okenia* has a whitish body color with red markings. *Okenia mexicorum* is similar to *O. mediterranea* (Ihering, 1886), the only other *Okenia* that has a prominent medial mid-dorsal ridge (Valdés and Ortea 1995). However, *O. mediterranea* lacks a papilla at the posterior end of the ridge and differs markedly in its radular and reproductive anatomy. In *O. mediterranea*, the inner lateral radular teeth (Schmekel and Portmann 1982; Valdés and Ortea 1995) have fewer denticles (12–14) than do those of *O. mexicorum* (26–34) and the curvature of the teeth of *O. mediterranea* is more gradual rather than being sharply angled as in *O. mexicorum*. The outer lateral teeth of *O. mediterranea* have a proportionately wider base and a shorter cusp than do those of *O. mexicorum*. The vaginal duct of *O. mexicorum* is very short, whereas it is elongate in *O. mediterranea* (Valdés and Ortea 1995). *Okenia hispanica* Valdés and Ortea, 1995, is white with pink and yellow spots, but it lacks a medial ridge and a medial papilla.

#### ACKNOWLEDGMENTS

This research has been supported by a grant from the National Science Foundation, PEET Program (DEB-9978155). Fieldwork was supported by the California Academy of Sciences. Specimens were also collected by several colleagues including Alicia Hermosillo, Orso Angulo Campillo, Sandra Millen, Luis Aguilar, Bob Van Syoc, Mike Ghiselin and Mike Miller. Their assistance and support are greatly appreciated.

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# A New Species of *Okenia* (Gastropoda: Nudibranchia: Goniadorididae) from the Pacific Coast of Costa Rica

Yolanda E. Camacho-García<sup>1</sup> and Terrence M. Gosliner<sup>2</sup>

<sup>1</sup> Instituto Nacional de Biodiversidad (INBio), Unidad de Malacología Apdo. 22-3100 Santo Domingo de Heredia, Costa Rica. Email: ycamacho@inbio.ac.cr; <sup>2</sup>Department of Invertebrate Zoology and Geology, California Academy of Sciences, 875 Howard Street, San Francisco, California 94103, USA. Email: tgosliner@calacademy.org

A new species of opisthobranch mollusk of the genus *Okenia* is described from the Pacific Coast of Costa Rica. *Okenia academica* sp. nov. has a translucent gray-brown body, and short dorsal tubercles, nine pairs of mantle processes which are white in color with orange to brick red apices. The species is compared to other species from the Panamic Province and the West coast of North America. This is the first record of the genus for the Pacific Coast of Costa Rica.

**Key words:** Mollusk, Nudibranchia, Costa Rica, *Okenia*.

## RESUMEN

Una nueva especie de molusco opistobranquio del género *Okenia* es descrito de la costa pacífica de Costa Rica. *Okenia academica* sp. nov. tiene un cuerpo gris cafésuzco traslúcido, nueve procesos en el manto, blancos en color con ápices anaranjados o rojo ladrillo y tubérculos cortos presentes en el dorso. La especie es comparada con otras especies de la Provincia Panámica y la costa Oeste de Norte América. Este es el primer registro del género para la costa pacífica de Costa Rica.

The genus *Okenia* Menke, 1830 consists of 10 species found primarily along the Pacific Coast of the Americas: *Okenia vancouverensis* O'Donoghue, 1921 from Canada, *Okenia plana* Baba, 1960 from California and Japan, *Okenia angelensis* Lance, 1966 from California and México, *Okenia* sp. 1 and *Okenia* sp. 2 (in Behrens 2004) from California, *Okenia luna* Millen, Schrödl, Vargas and Indacochea, 1994 from Perú and Chile, and three other new species from México (Gosliner & Bertsch, 2004). Another species, *Hopkinsia rosacea* MacFarland, 1905 has recently been placed within the genus *Okenia* (Gosliner, 2004). The description of the present species is the first report and description of a member of the genus *Okenia* for the Pacific Coast of Central America.

## SPECIES DESCRIPTION

### Genus *Okenia* Menke, 1830

Type species: *Doris elegans* Bronn, 1826

### *Okenia academica* Camacho-Garcia and Gosliner, sp. nov

(Figs. 1–3)

**TYPE MATERIAL.**—HOLOTYPE: Punta San Francisco, Playa Tamarindo, Parque Nacional Las

Baulas, Area de Conservación Tempisque, Costa Rica ( $9^{\circ}03'58''\text{N}$ ,  $85^{\circ}51'08''\text{W}$ ), January 12, 2001, 1 specimen, dissected, 6 mm preserved length, 0 meters depth, leg. J. Magaña (INB0003118102); SEM stub with radula and jaw (INB0003764988); PARATYPES: Punta San Francisco, Playa Tamarindo, Parque Nacional Las Baulas, Area de Conservación Tempisque, Costa Rica ( $9^{\circ}03'58''\text{N}$ ,  $85^{\circ}51'08''\text{W}$ ), January 12, 2001, 1 specimen, dissected, 6 mm preserved length, 0 meters depth, leg. J. Magaña (CASIZ 170030), with the radula mounted on a SEM stub with the same number; San Miguel, Reserva Natural Absoluta de Cabo Blanco, Area de Conservación Tempisque, Costa Rica ( $9^{\circ}34'53''\text{N}$ ,  $85^{\circ}08'26''\text{W}$ ), September 18, 1998, 1 specimen, 3 mm preserved length, 0 meters depth, leg. F. Alvarado (INB0001496648).

**GEOGRAPHIC RANGE.**— This species is known only from the Pacific Coast of Costa Rica (present study).

**ETYMOLOGY.**— The species is named after the California Academy of Sciences (CAS) in San Francisco, California to honor its contribution to the inventory of opisthobranch mollusks in Costa Rica and to honor the celebration of its sesquicentennial.

**EXTERNAL MORPHOLOGY.**—

The body is oval and elongated (Fig 1A–B). The dorsum has as many as 24 small tubercles of different sizes. There are no spicules present on the notum. The head has the form of a bilobed velum (Fig. 2B). The rhinophores are proportionally very long with respect to the length of the animal and curve backwards with about 18 fine lamellae. There are two notal processes above the veil and seven elongated notal papillae on each side of the body that can curl either inward or upward. The last process on each side of the body is much longer and bifid.

The branchial leaves are larger anteriorly. The branchial plume is composed of 10 to 13 unipinnate branchial leaves. The anal papilla is located in the center of the branchial leaves. The viscera are visible through the notum in the anterior part of the body. The prolongation of the pointed foot is visible when the animal is in motion. The foot is simply rounded anteriorly.

The background color of the body is translucent gray-brown.

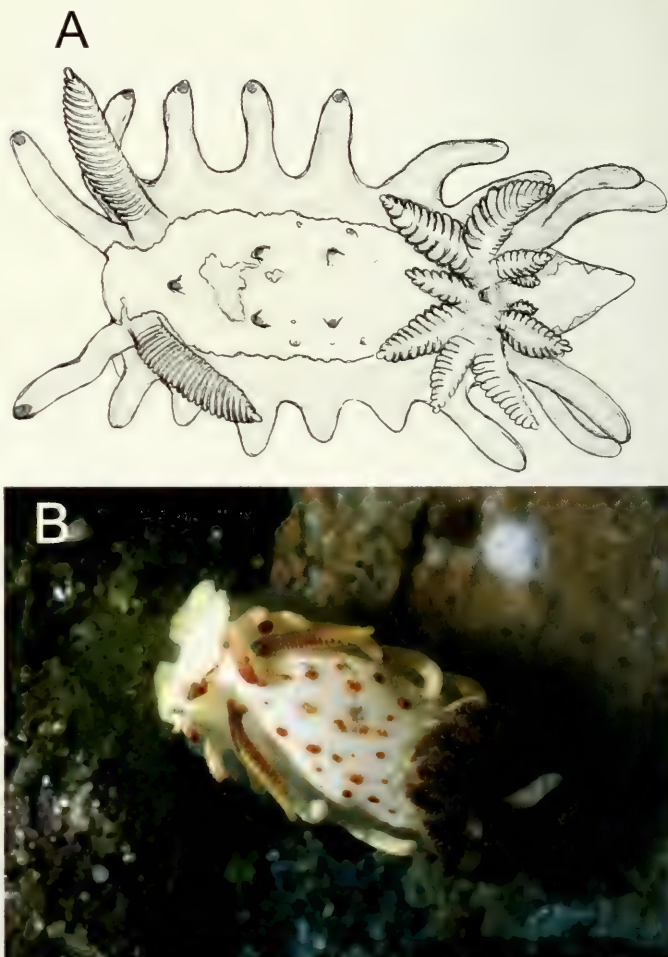


FIGURE 1. A. Drawing of the living animal of *Okenia academica* sp. nov., Costa Rica (INB003118104). B. Photograph of the living animal of *Okenia academica* sp. nov., Costa Rica (INB003118104).

The notum and the greater ventral part of the foot are opaque white. The largest tubercles in the center of the back are reddish brown to reddish orange in color (Fig. 1A–B). The rhinophores and gill range from translucent white to reddish brown with small white opaque spots. The apices of the lateral processes are orange to brick red. The anus is reddish brown. The anterolateral corners of the foot are white translucent with some yellowish spots. Ventrally, the foot is translucent gray.

**ANATOMY.**— The buccal bulb is large and muscular (Fig. 2A). The buccal pump is large and expands dorsally and posteriorly. A pair of short salivary glands is present adjacent to the entrance of the elongate, thin esophagus. The radular sac descends ventrally from the buccal mass.

The radular formula is 36 x (1.1.0.1.1) in a 6 mm preserved length specimen (Fig 3A). The inner lateral teeth have up to 28 strong denticles on the inner surface of the masticatory border (Fig 3C–D). Each outer lateral tooth has one cusp (Fig 3B). The labial disc is composed of several rectangular jaw elements which are homogeneously distributed (Fig 3E). Each of the jaw elements bears up to six irregular serrations on the outer edges (Fig 3F).

The ampulla is very long and thick. It divides into a short oviduct that enters the female gland mass near the lower right side of the mass and the prostate (Fig. 2C). The prostate is long, tubular

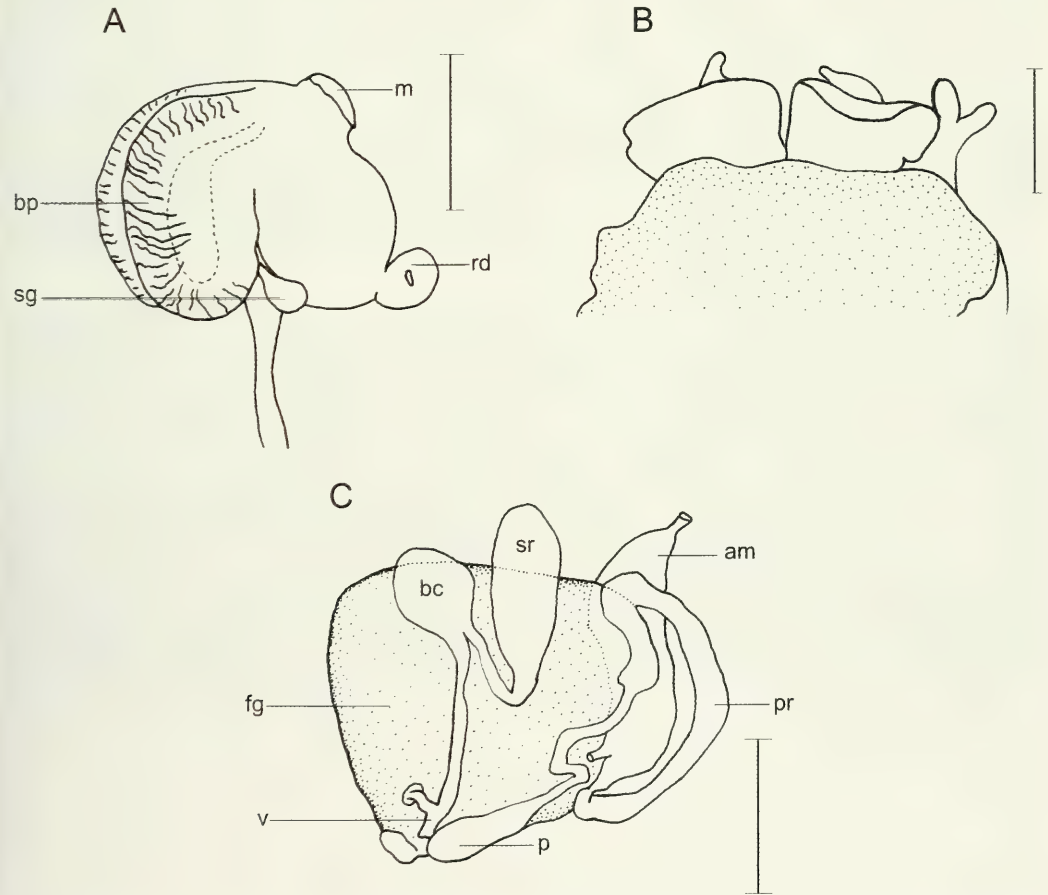


FIGURE 2. A. Buccal mass from right side of *Okenia academica* sp. nov., scale bar= 1 mm. Abbreviations: m= mouth; rd = radular sac; bp= buccal pump; sg = salivary gland. B. Head of *Okenia academica* sp. nov., scale bar= 1 mm. C. Reproductive system of *Okenia academica* sp. nov., scale bar= 1 mm, Abbreviations: am=ampulla, bc=bursa copulatrix, fg=female gland, p= penis, pr=prostate, sr=seminal receptacle, v=vagina.



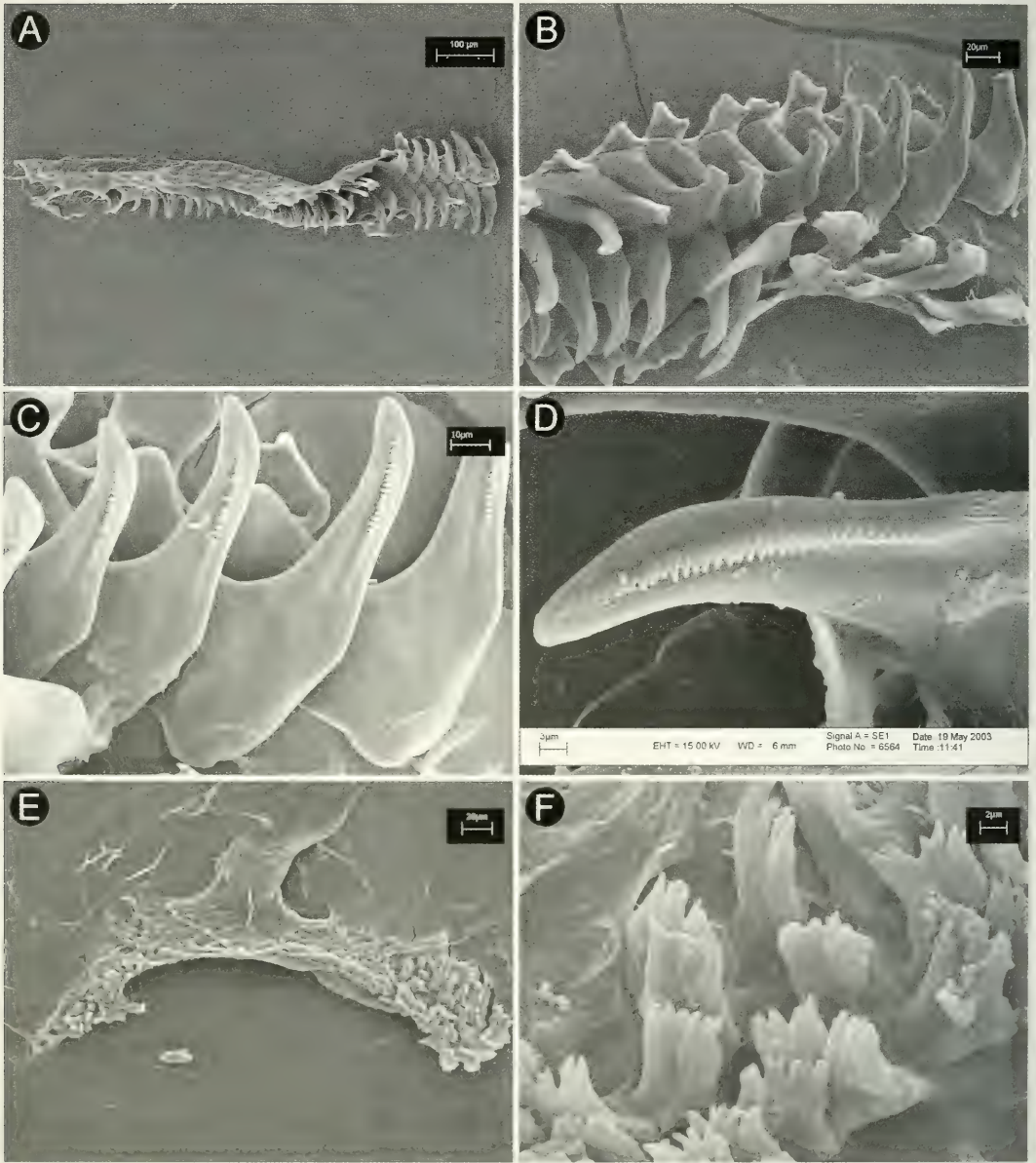


FIGURE 3. Scanning electron micrographs of *Okenia academica* sp. nov. A. Radula (INB003118102). B. Lateral and marginal teeth (INB0003118104). C. Detail of the lateral teeth (INB0003118104). D. Detail of the denticles of a lateral tooth (INB003118102). E. Jaw (INB003118102). F. Detail of the jaw elements showing the serrated edge (INB003118102).

and convoluted near the middle section. It constricts into a thin, tubular and muscular vas deferens that forms a slight loop into itself. The distal part of the vas deferens is inside a pear-shaped penis. No penial spines were observed in the slide preparation of the penis. The vagina is very long. Near its base, the uterine duct branches and enters the female gland mass. More proximally, it enters the oval bursa copulatrix. A shorter duct emerges from the base of the bursa copulatrix and leads to an

oval and elongate seminal receptacle. The seminal receptacle is twice as large as the bursa copulatrix.

**REMARKS.**— The seven species of *Okenia* known to inhabit the Pacific Coast of North America have been reviewed recently (Gosliner and Bertsch 2004), this review included three new species. Of the four species that had already been described, *O. rosacea* (MacFarland, 1905), and *O. plana* Baba, 1960, differ from the present species in lacking a distinct lateral side of the body separate from the notum and foot. *Okenia vancouverensis* (O'Donoghue, 1921) differs from *O. academica* in its external body color, being brown with opaque white spots and in having shorter lateral papillae. *Okenia angelensis* Lance, 1966, has an elongate body with a yellowish color ornamented with brown spots. It has only two to three rhinophoral lamellae in contrast to the 18 found in *O. academica*. The three new Mexican species also differ from *O. academica*. *Okenia cochimi* Gosliner and Bertsch, 2004, has a uniformly yellow body color with a single elongate medial notal papilla anterior to the gill. *Okenia mexicorum* Gosliner and Bertsch, 2004, is opaque white with red markings and also has a single medial notal papilla anterior to the gill. (See also Table 1 for summary of diagnostic characters.)

The species that is most similar to *O. academica* is *Okenia angelica* Gosliner and Bertsch, 2004. Externally this species is similar in that it has a broad body with elongate lateral papillae and low tubercles on the notum. The two posteriormost pairs of papillae also originate from a common base in both species and both have a bilobed velum. However, there are significant differences as well. In *O. angelica*, the margins of the notum, foot, bases of the rhinophores, lateral papillae, tubercles, and gills are all covered with dark purple pigment. The middle of the notum is covered by opaque white as in *O. academica*, but the opaque white covers much less of the notal surface in *O. angelica*. In *O. angelica*, the lateral papillae are covered with light, opaque orange-white pigment and lack the darker orange apices of *O. academica*. Internally, the two species have similarly shaped radular teeth and jaw plates. The radula of *O. academica* contains 36 rows of radular teeth in a 6 mm specimen, while a 12 mm specimen of *O. angelica* had only 25 rows of teeth. The inner lateral teeth of *O. angelica* have a more elongate, acutely pointed cusp and have a few more denticles that are more widely spaced than are those of *O. academica*. The most significant differences between the two species are found in the morphology of the reproductive system. In *O. academica* the uterine duct emerges from near the base of the vagina, while in *O. angelica*, it emerges from the top of the vaginal duct at the base of the bursa copulatrix and receptaculum seminis. In *O. academica*, the receptaculum seminis is larger than the bursa copulatrix, while in *O. angelica*, the bursa is larger. In *O. academica* the prostate is much longer than the ejaculatory portion of the vas deferens, while in *O. angelica* the prostate is very short and the ejaculatory segment is very long. The penial sac of *O. academica* is wider than the ejaculatory duct, while in *O. angelica* they are about the same width.

*Okenia luna* Millen, Schrödl, Vargas and Indacochea, 1994 can be differentiated from *O. academica* externally by the number and color of the mantle processes, which are white with orange to brick red apices and the presence of several tubercles or papillae on the notum, and a notched foot. *Okenia luna* is characterized by a smooth dorsum, a white body with yellow markings, unnotched foot, and flat, triangle-shaped oral tentacles.

#### ACKNOWLEDGMENTS

This research was made possible by the Cooperative Agreement between the Ministry of Environment and Energy (MINAE) and Instituto Nacional de Biodiversidad (INBio). The field-work in Costa Rica was funded by the INBio through the Netherlands Government and the project

TABLE 1. Comparative morphology of the valid species of the genus *Okenia* from the Panamic Province and

<i>Species</i>	<i>Description source</i>	<i>Distribution</i>	<i>Dorsal color</i>	<i>Ventral color</i>	<i>Velar appendages per side</i>
<i>Okenia rosacea</i> (MacFarland, 1905)	MacFarland 1905; Gosliner, 2004	Oregon to Isla San Martín Baja Calif	rose pink	pink	twelve, pink
<i>Okenia vancouverensis</i> O'Donoghue, 1921	O'Donoghue, 1921; Gosliner and Bertsch, 2004	Canada	Brownish with opaque white spots and opaque white medial line on foot	unknown	one, same color as the body
<i>Okenia plana</i> Baba, 1960	Baba, 1960; Rudman and Darvell, 1990; Bouchet and Ortea, 1993; Gosliner, 2004	Japan, Philippines, Hong Kong, New Zealand, Australia, introduced into California	translucent yellowish white, small brown spots	translucent white	one, speckled with dark brown
<i>Okenia angelensis</i> Lance, 1966	Lance, 1966; Behrens, 1991 and Muñoz et.al. 1996; Schrödl, 2003	California to Chile	translucent white flecked with small yellowish and white granules. Reddish brown and green spots also present	sparsely speckled w/light yellow & white	one, white
<i>Okenia luna</i> Millen, Schrödl, Vargas, and Indacochea 1994	Millen, Schrödl, Vargas, and Indacochea 1994; Schrödl, 2003	Perú and Chile	hyaline white with a mid-dorsal stripe of yellow spots	hyaline white usually without pigment	one, yellow
<i>Okenia angelica</i> Gosliner and Bertsch, 2004	Gosliner and Bertsch, 2004	Bahía de Los Angeles to Bahía Banderas, México	deep purplish with opaque white on the center of the notum	translucent white	two, with white apices
<i>Okenia cochimi</i> Gosliner and Bertsch, 2004	Gosliner and Bertsch, 2004	Isla Cedros to Bahía Ballena, México	uniformly lemon yellow	translucent white	one, lemon yellow
<i>Okenia mexicorum</i> Gosliner and Bertsch, 2004	Gosliner and Bertsch, 2004; Behrens, 1991	Baja California Sur to Bahía de Banderas, Jalisco	opaque white patch with reddish brown patches	translucent white	two, reddish brown
<i>Okenia academica</i> Camacho-García and Gosliner, sp. nov	present paper	Costa Rica	translucent gray-brown	translucent gray	one, with orange to brick red apices

Note: P=present; A=absent; N=notched; U=unnotched

"Development of Biodiversity Knowledge and Sustainable Use in Costa Rica." This paper is supported in part by the National Science Foundation through the PEET grant DEB-9978155, "Phylogenetic systematics of dorid nudibranchs," to Terrence M. Gosliner and Ángel Valdés and the California Academy of Sciences. Ángel Valdés made the drawing of the specimens from Costa Rica and Maribel Zúñiga helped with some technical aspects of the paper. David Butvill made constructive comments on this manuscript.



from Western North America.

Mantle processes per side	Rhinophoral bases	Branchial leaves	Dorsal papillae	Oral tentacles	Foot	Cusps of outer lateral teeth	Jaws	Radula
numerous, pink	reddish pink	reddish pink	numerous, pink	A	N	reduced to a small plate	P, short	16-22 x (1.1.0.1.1)
9-10 pairs laterally	same color as the body	same color as the body	P, 24 papillae on the notum	P, digitiform rounded tips	U, broad	one single prominent cusp	P	32 x (1.1.0.1.1)
4, speckled in dark brown	translucent white	translucent white with dark brown specks	P, one medial with brown specks	A	N	two cusps, occasionally with 2-3 smaller denticles	P, regular rounded	21-29 x (1.1.0.1.1)
6-7, white	white w/yellow & white specks at distal end; brown specks near base	white with yellow and brown flecks	P, five or six	P, pointed and fleshy	U	two prominent cusps	A, no distinct jaw plates	21 x (1.1.0.1.1) 19 x (1.1.0.1.1)
8-10, yellow	hyaline white bases, cream leaves w/ opaque white pigment	hyaline white with a yellow streak	A	P, broad, flattened triangles	U	one small cusp	P, rectangular with six serrations	23-27 x (1.1.0.1.1)
6-7 w/white apices	purple	with dark brown apices	P, many rounded tubercles, brown in color	P, broad	U	no distinct cusp	P, rectangular with 2-4 serrations	25 x (1.1.0.1.1)
4-7 w/lemon apices	lemon yellow	lemon yellow	P, 1 medial lemon yellow	P, rounded	U	one single and curved	P, small irregular polygonal plates	13 x (1.1.0.1.1)
6-9 reddish brown, some w/opaque white apices	white	translucent white with reddish brown pigment	P, one medial reddish brown with white apex	P, rounded	U	one single and curved	P, very weakly developed	15 x (1.1.0.1.1)
7 w/orange to brick red apices	translucent with small white opaque spots or very dark reddish brown color	translucent w/small white opaque or dark reddish brown spots	P, reddish brown to reddish orange in color	P, broad	U	one small cusp	P, rectangular with six serrations	36 x (1.1.0.1.1)

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**A New Species of *Schizobopyrina* Markham, 1985  
(Crustacea: Isopoda: Bopyridae: Bopyrinae) Parasitic  
on a *Gnathophyllum* Shrimp from Polynesia, with  
Description of an Associated Hyperparasitic Isopod  
(Crustacea: Isopoda: Cabiropidae)**

**Jason D. Williams<sup>1,3</sup> and Christopher B. Boyko<sup>2</sup>**

<sup>1</sup> Department of Biology, Hofstra University, Hempstead, New York 11549, U.S.A.;

<sup>2</sup> Division of Invertebrate Zoology, American Museum of Natural History,  
Central Park West at 79th St., New York, New York 10024, U.S.A.

A male and female bopyrid pair was found in the branchial chamber of a bumblebee shrimp, *Gnathophyllum americanum* Guérin-Méneville, collected from Tonga. Examination of these specimens showed that they belong to the bopyrid genus *Schizobopyrina* Markham, but cannot be placed in any of the described species. We describe this new species as *S. bombyliaster* and compare it to the other species in the genus. This is the first described species of branchial bopyrid from the genus *Gnathophyllum*, and only the second bopyrid described from a member of the Gnathophyllidae. The marsupium of the female bopyrid contained specimens of a new species of the hyperparasitic isopod genus *Cabirops* Kossmann, which is described based on light and scanning electron microscope investigations and discussed in relation to other species in the genus.

Bopyrid isopods of the subfamily Bopyrinae are obligate parasites found in the branchial chambers of caridean shrimp (Decapoda: Caridea). The genus *Schizobopyrina* Markham, 1985, was erected for species formerly placed in *Bopyrina* Kossmann, 1881, but which possess a maxilliped palp, elongate oostegites 2–5, and lateral or complete separation of the pleomeres of the female.

A single parasitized specimen of *Gnathophyllum* shrimp (Fig. 1) was found by one of us (CBB) in the collections of the California Academy of Sciences and was identified as belonging to the widespread species *G. americanum* Guérin-Méneville. Examination of the bopyrid parasites showed they belong to an undescribed species of *Schizobopyrina*. In addition, the female specimen of *Schizobopyrina* was hyperparasitized by specimens of a new species of isopod of the genus *Cabirops* Kossman, 1872. The only other described species of bopyrid isopod on a member of *Gnathophyllum*, or the family Gnathophyllidae, is the abdominal species *Diplophryxus kemp* Chopra, 1930 (Hemiarthrinae), from *G. americanum* (originally as *G. fasciolatum* Stimpson) collected in the Andaman Islands. A branchial bopyrid on *G. modestum* Hay in the Gulf of México was reported by Dardeau et al. (1980; repeated by Markham 1985), but was never identified even to the subfamily level. All other hosts of *Schizobopyrina* species are in either the Palaemonidae, which with the Gnathophyllidae forms part of the Palaemonoidea, or the Hippolytidae (Alpheoidea).

<sup>3</sup> Contact author: biojdw@hofstra.edu



## METHODS

Camera lucida sketches made of specimens were scanned into a Macintosh™ computer. Images were then prepared using the programs Adobe Photoshop™ and Adobe Illustrator™. For Scanning Electron Microscopy (SEM), the male *Cabirops* specimen was dehydrated in an ascending ethanol series followed by four changes of 100% ethanol. Dehydration was completed with a Samdri 795 Critical Point Drier. The dried specimen was mounted on an aluminum stub, coated with gold (EMS-550 Sputter coater), and viewed with a Hitachi S-2460N SEM.

Carapace length (CL), including the rostrum, is provided as an indicator of size for the host shrimp. Isopod size is given as total body length (anterior margin of head to posterior margin of pleotelson). Measurements were made to 0.01 mm using an ocular micrometer.

All specimens are deposited in the Division of Invertebrate Zoology, California Academy of Natural Sciences, San Francisco, U.S.A (CASIZ), except for the specimen of *Schizobopyrina gracilis* (Chopra, 1923), which is in the Museum National d'Histoire Naturelle, Paris (MNHN).

## DESCRIPTIONS OF TAXA

**Family Bopyridae Rafinesque-Schmaltz, 1815**  
**Subfamily Bopyrinae Rafinesque-Schmaltz, 1815**

**Genus *Schizobopyrina* Markham, 1985**

***Schizobopyrina bombyliaster* Williams and Boyko, new species**  
(Figs. 1-4)

**MATERIAL EXAMINED.**—Holotype: female (4.41 mm), infesting right branchial chamber of female *Gnathophyllum americanum* (3.71 mm CL; CASIZ 170233), 18°43'S, 174°05'E, on coral reef to coral rubble on sand bottom, leeward side of reef, north side of reef between Langitau and Vaka'eitu Island, Vava'u Island Group, Tonga, 2–10 ft (= 0.6–2.7 m) depth, hyperparasitized by *Cabirops bombyliophila* sp. nov. (CASIZ 170231–170232), coll. Van Syoc, Ferreira, Campbell, and Cornfield, 30 July 1985 (CASIZ 5707). Allotype: male (1.04 mm), same data as holotype (CASIZ 170234).

**TYPE LOCALITY.**—18°43'S, 174°05'E, leeward side of reef, north side of reef between Langitau and Vaka'eitu Island, Vava'u Island Group, Tonga, Pacific Ocean, 0.6–2.7 m depth.

**DESCRIPTION.**—Female (Figs. 2–3). Body length 4.41 mm, maximal width 2.34 mm, head length 0.94 mm, head width 1.01 mm, pleon length 1.31 mm. Pereon and pleon deflexed dextrally. Body outline of pereon broad anteriorly, tapering posteriorly; pleon subequal to posterior pereon. All body regions and pereomeres distinctly segmented (Fig. 2A–B).

Cephalon triangular, tapering posteriorly, median region strongly delineated; well withdrawn into first pereomere, nearly obscuring median of first pereomere; frontal lamina strong, triangular, width approximately one-half of head and distinctly separated from head. Eyes lacking. Antenna and antennule (Fig. 3B) of 3 articles each, distal margin of distal segments with setae. Maxilliped (Fig. 3C) with narrow rounded spur; palp single segmented and non-articulated with 7 thick elongate setae at distal margin.

Pereon composed of 7 pereomeres, broadest across pereomere 3, tapering anteriorly and posteriorly. All pereomeres separated. Coxal plates on sides of pereomeres all similar, indistinct; dorsolateral bosses produced on pleomeres 1–4, strongest on 2–4 and larger on right side of body (Fig. 2A). Oostegites enclosing only approximately one-fourth of brood pouch (Fig. 2B); first oostegit-

es asymmetrical, right one slightly smaller, with posterolateral lobe extended, smoothly angled, distal end rounded, not setose (Fig. 3D), left one with posterolateral lobe short, sharply angled, distal end setose (Fig. 3E). Pereopods (Figs. 2A, 3F–G) of about same size. Propodus of all pereopods with shallow cup-like insertion for dactylus (Fig. 3F); distoventral margin of carpus with numerous scales and few short setae at distal tip. First 2 pereopods surrounding head region; no large gaps between any pereopods.

Pleon with 5 distinct pleomeres. Pleomeres 1–4 increasingly concave on median of posterior margin, with extended ovate, distally tapering and acute, biramous pleopods and uniramous, distally produced and rounded lateral plates (Figs. 2B, 3A); pleomere 5 fused with pleotelson (Figs. 2A), anteriorly sharply convex and posteriorly straight, lacking pleopods and with subquadrate, distally directed, lateral plates; uropods lacking (Fig. 2A).

Male (Fig. 4). Length 1.04 mm, maximum width 0.40 mm, head length 0.15 mm, head width 0.27 mm, pleon length 0.29 mm. Occurring on ventral surface of female's pleon between pleopods (Fig. 2A); directed anteroposteriorly.

Head anterior margin subovate, posterolateral margins slightly concave, posterior margin straight, widest medially, incompletely fused with 1st segment of pereon. Moderate sized eyes located mediolaterally. Antenna and antennule of 2 articles each (Fig. 4C), distally setose; extending posterolaterally from head, not overreaching margins of head.

Pereomere 3 broadest, tapering slightly anteriorly and posteriorly. Pereomeres 1–3 directed laterally; 4–7 with posterolateral margins directed slightly posterolaterally. Body lacking pigmentation. All pereopods (Fig. 4D–E) of subequal size, all articles distinctly separated; distoventral surfaces of propodus and carpus with large flat scales and few short setae.

Pleon tapering posteriorly, pleomeres directed laterally and fringed with setae. All segments fused, but with deep lateral indentations and faint dorsal suture lines demarcating segments. No

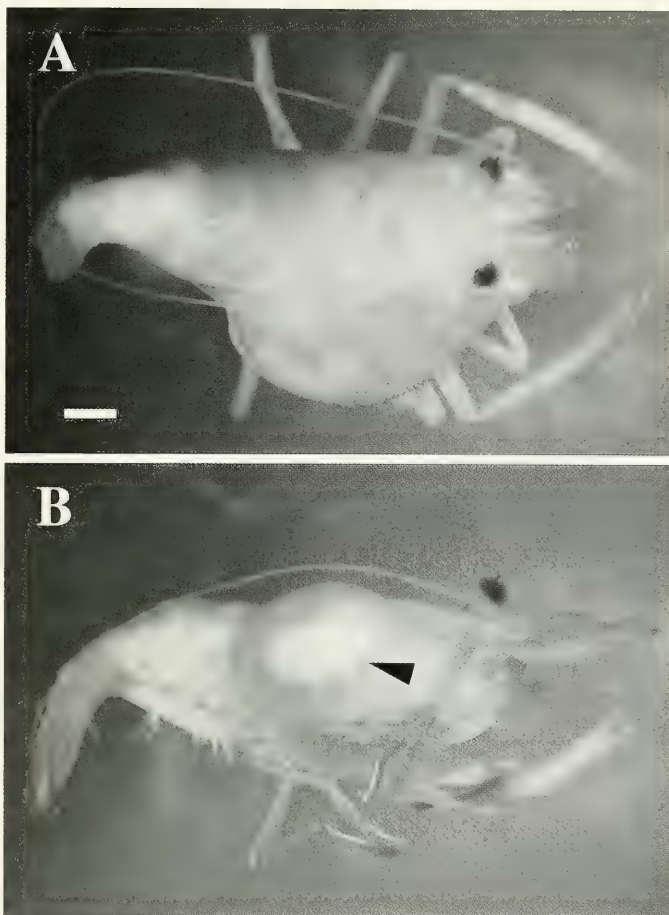


FIGURE 1. The bumblebee shrimp (*Gnathophyllum americanum*) harboring *Schizobopyrina bombyliaster* sp. nov. and *Cabirops bombyliophyla* sp. nov. in right branchial chamber, CASIZ 170233 (shrimp), 5707 (female bopyrid), 170232 (female cabiropid). A, dorsal view; B, lateral view (arrowhead indicates *Cabirops* female within brood chamber of *Schizobopyrina* female). Scale = 1.0 mm.

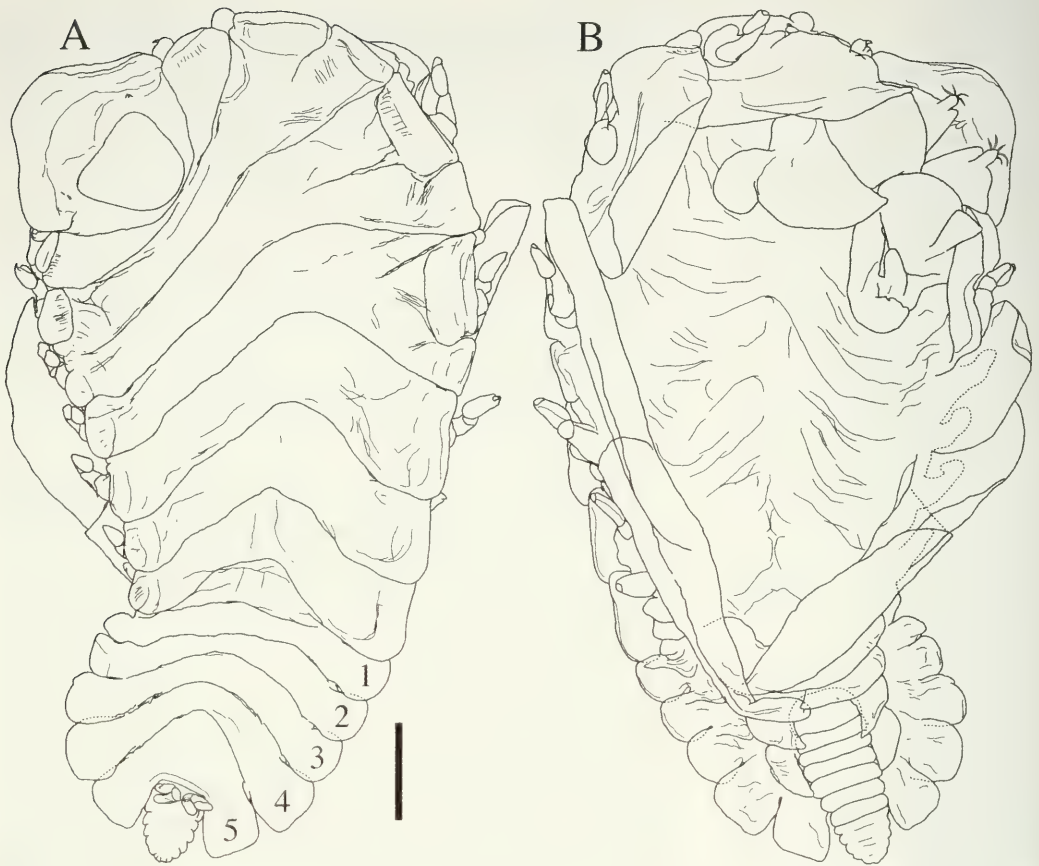


FIGURE 2. *Schizobopyrina bombyliaster* sp. nov., female, 4.41 mm, CASIZ 5707, holotype (with male *in situ*). A, dorsal view; B, ventral view. Numbers indicate pleomere. Scale = 500  $\mu$ m.

midventral tubercles; 5 pairs of subquadrate tuberculiform pleopods, last pair markedly smaller and more ovate than other pairs (Fig. 4B). Pleotelson (Fig. 4A–B) slightly produced medially, with sinuous lateral margins, uropods absent.

**DISTRIBUTION.**— Found on the shrimp, *Gnathophyllum americanum* from Tonga; 0.6–2.7 m depth.

**ETYMOLOGY.**— The specific name, literally bumblebee-eater, is given to call attention to the occurrence of this parasite on a bumblebee shrimp of the genus *Gnathophyllum*.

**REMARKS.**— Of the 12 other species currently placed in *Schizobopyrina* (see Campos and Campos 1990), this new species most closely resembles *S. gracilis* (Chopra, 1923). The female of *S. gracilis* reported by Bourdon (1983, as *Bopyrina gracilis*) was examined for comparison to the material from Tonga, as the types of *B. gracilis* are in the Zoological Survey of India and unavailable for examination. Bourdon's (1983) specimen (MNHN-Ep 347, female 1.88 mm, Amboine (= Ambon, Indonesia) coll. Rumphius II, 1975, ex *Periclimenes tenuis* Bruce) corresponds well with the type of *S. gracilis* as described and figured by Chopra (1923), although the lateral plates and dorsal segmentation of the pleomeres are even less distinctly separated in the Ambon specimen. Unfortunately, the male specimen from Ambon has become lost and could not be examined, but all the characters given for it by Bourdon (1983) match those of the male type of *S. gracilis*.



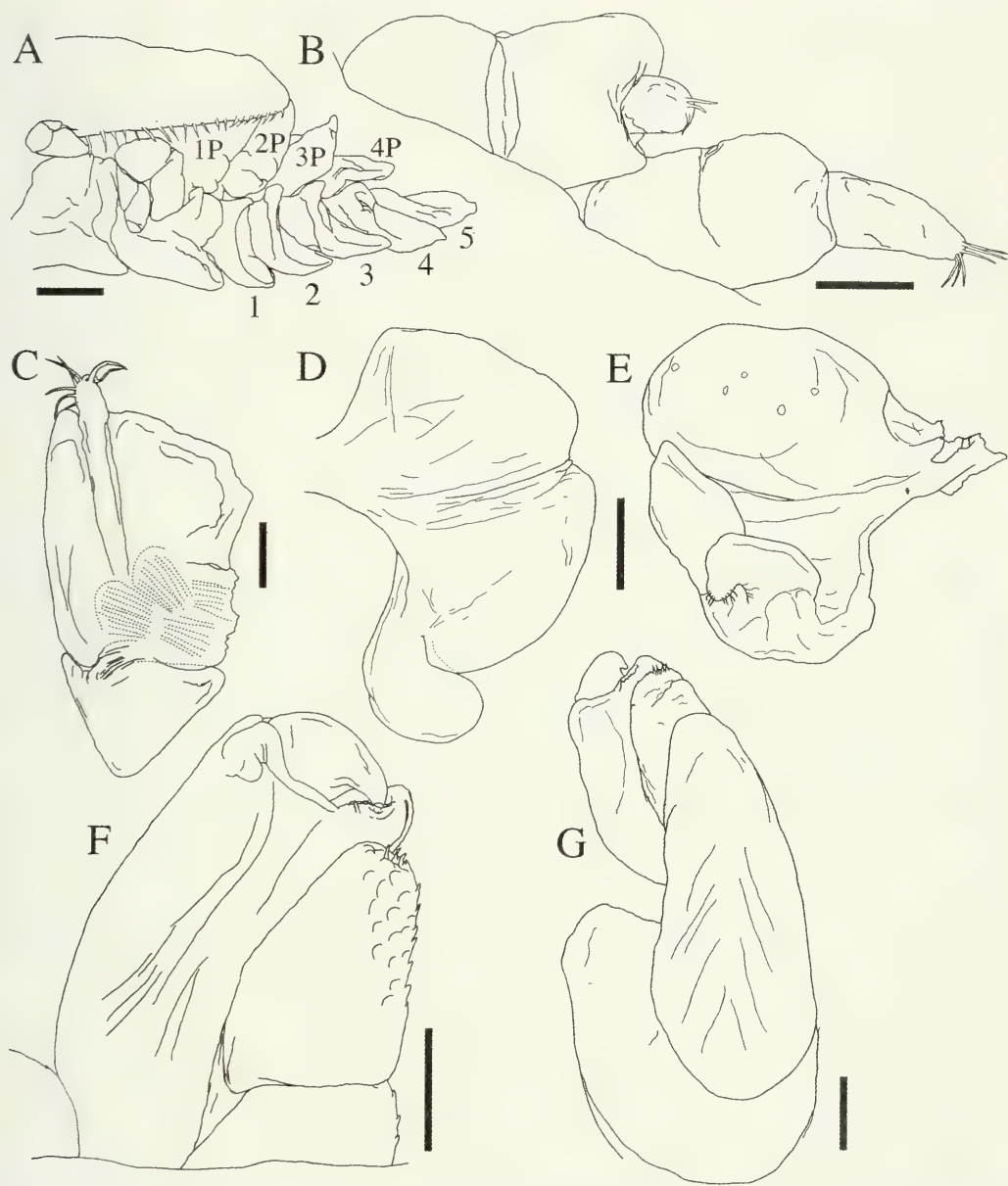


FIGURE 3. *Schizobopyrina bombyliaster* sp. nov., female, 4.41 mm, CASIZ 5707, holotype. A, posterolateral view, left side (P=pleopod; numbers indicate pleomere); B, left antenna and antennule; C, left maxilliped, external view; D, right oostegite 1, external view; E, left oostegite 1, external view; F, right pereopod 7; G, right pereopod 2. Scale = 250 µm (A), 500 µm (B), 150 µm (C), 250 µm (D, E), 50 µm (F-G).

The female of *S. bombyliaster* sp. nov. resembles *S. gracilis* in the overall shape of the head, the number of pleomeres (pleomere 5 fused with pleotelson), and the shape of the posterior margin of the pleomere 5/pleotelson. It differs from *S. gracilis* in that the frontal lamina of the head and the dorsolateral bosses on the pereomeres are much more developed, the pleomere segments are distinct, the lateral plates on pleomeres 1–4 are much more separated, and the lateral plates of

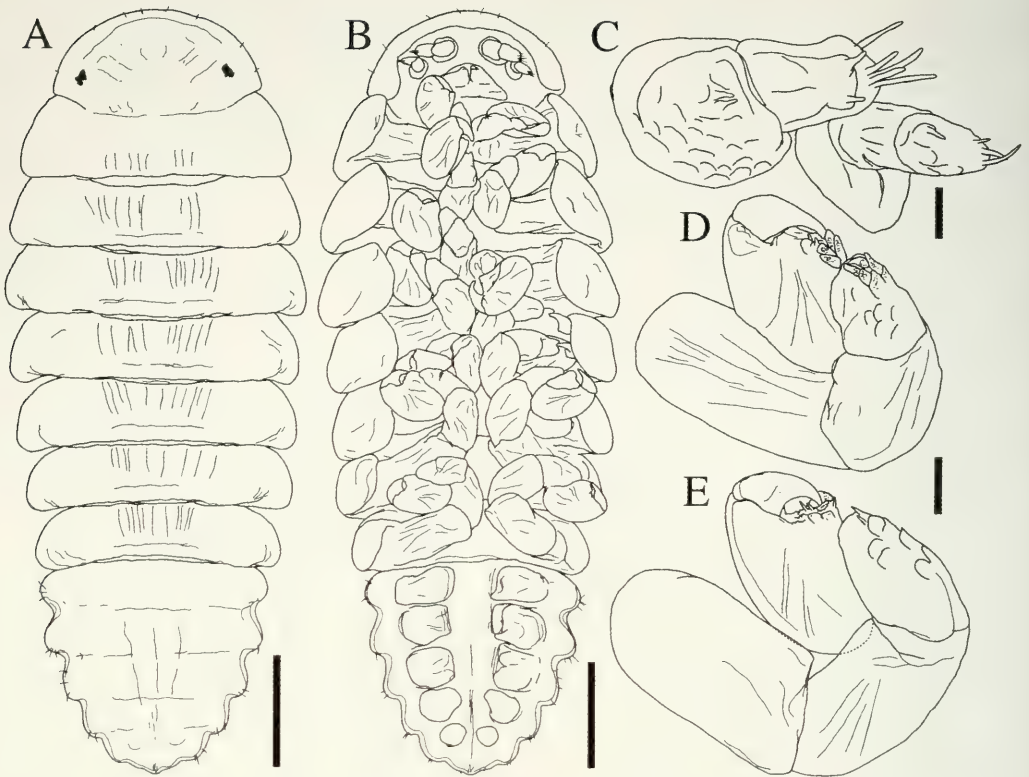


FIGURE 4. *Schizobopyrina bombyliaster* sp. nov., male, 1.04 mm, CASIZ 170234, allotype. A, dorsal view; B, ventral view; C, left antenna and antennule; D, right pereopod 1; E, right pereopod 7. Scale = 150  $\mu$ m (A–B), 125  $\mu$ m (C), 250  $\mu$ m (D–E).

pleomere 5/pleotelson are subquadrate instead of rounded. The shape of the left oostegite 1 is also quite different from that of *S. gracilis* or any other *Schizobopyrina* species. The male of *S. bombyliaster* sp. nov. is very much like that of *S. gracilis*, but the posterior margin of the pleotelson is only slightly produced, while that of *S. gracilis* is strongly produced.

The genus *Schizobopyrina* now contains 13 species, although we concur with Campos and Campos (1990) that *S. lobata* Bourdon and Bruce, 1983, does not appear to belong to this genus. *Schizobopyrina bombyliaster* sp. nov. belongs to the group of *Schizobopyrina* with females having pleomere 5 partly or wholly fused with the pleotelson that also includes *S. amakusaensis* (Shiino, 1939), *S. andamanica* (Chopra, 1923), *S. bruscai* Campos and Campos, 1990, *S. gracilis* (Chopra, 1923), and *S. miyakei* (Shiino, 1942). Both Chopra (1923) and Campos and Campos (1990) described *S. andamanica* (as *andamica* [sic] in Campos and Campos [1990]) and *S. gracilis* as having 5 pleomeres plus pleotelson, but the illustrations of Chopra (1923) clearly show only slight lateral distinction between the segments in some specimens of *S. andamanica* (Chopra 1923: pl. 20, fig. 1, text-fig. 28) and no discernable distinction in *S. gracilis* (Chopra 1923: pl. 21, fig. 6). This is in agreement with the specimen of *S. gracilis* reported by Bourdon (1983) and unlike the clear separation of those segments in all other *Schizobopyrina* species.

**Family Cabiropidae Giard and Bonnier, 1887****Genus *Cabirops* Kossmann, 1872*****Cabirops bombyliophila* Williams and Boyko, new species**

(Figs. 1, 5–8)

**MATERIAL EXAMINED.**—Holotype: male (0.91 mm) infesting female *Schizobopyrina bombyliaster* sp. nov. (4.41 mm; CASIZ 5707) ex *Gnathophyllum americanum* (3.71 mm CL; CASIZ 170233), 18°43'S, 174°05'E, on coral reef to coral rubble on sand bottom, leeward side of reef, north side of reef between Langitau and Vaka'eitu Island, Vava'u Island Group, Tonga, 2–10 ft (= 0.6–2.7 m) depth, coll. Van Syoc, Ferreira, Campbell, and Cornfield, 30 July 1985 (CASIZ 170231). Allotype: immature female (2.36 mm), same data as holotype (CASIZ 170232).

**TYPE LOCALITY.**—18°43'S, 174°05'E, leeward side of reef, north side of reef between Langitau and Vaka'eitu Island, Vava'u Island Group, Tonga, Pacific Ocean, 0.6–2.7 m depth.

**DESCRIPTION.**—Male (Figs. 5–7). Length 0.91 mm, maximum width 0.41 mm at segment 4, head length 0.11 mm, pleon length 0.41 mm; body tear-drop shaped. Cuticular surface with distinct striations, prominent on coxal plates (Fig. 6C–D).

Head anterior margin ovate, posterior margin convex, widest at posterolateral junction with segment 1 (Figs. 5A, 6A–B). Subovate, moderately large eyes (approximately 60  $\mu$ m in maximal length) located mediolaterally, eyes with irregular pigment most prominent around medially directed edge (Fig. 5A). Antenna of 3 articles (Fig. 5C), first article with 3 setae near anterolateral border, article 1 slightly overlaps basal article of antennule, article 2 with series of shelves, 4 setae on distal margin of article 2, distal bundles of long setae on antenna extend to segment 1, extending slightly beyond margin of head (Fig. 5B). Antennule of 9 articles (4 peduncular and 5 flagellar) (Fig. 5B), first article with rounded anterior edge, articles 1 and 2 with apophysis on posteromedial edge, articles 3 and 4 lacking apophysis; flagellar articles much narrower than peduncular articles, each with a terminal seta, proximal flagellar article shortest, flagellar articles 2–5 of increasing length, article 5 with approximately 2 long and 2 short, distal setae.

Pereomere 4 broadest, tapering anteriorly and posteriorly. Body pigmentation lacking. Pereomeres with toothed coxal plates; three denticles in plates 1–5, 1 denticle in plates 6–7 (Figs. 5B; 6C–E), medial tooth largest in all segments, lateral two teeth with rounded distal end, diminishing in size over segments 1–5 (Fig. 6C–E). Pereopods 1 and 2 gnathopodal with bifid dactyli (Fig. 7A–C); distoventral surfaces of propodus and carpus with large flat scales and a few setae, rows of minute setae along distal edge of propodus around joint with dactylus, with setae along edge apposed to dactylus, three stout setae on propodus near tip of dactyl (Fig. 7A–C). Pereopods 3–7 ambulatory, carpi of pereopods 3–7 with one stout terminal seta, proprodi with long axis curved, inner margins with two (pereopods 3–5) or one (pereopods 6 and 7) stout setae toward distal end (Figs. 5B; 7D–F) and comb of minute setae along edge (Fig. 7F), dactyli of pereopods 3–7 with long axis curved, tapering to a sharp point (pereopods 3–5), or blunt tip (pereopods 6 and 7), with comb of minute setae (Fig. 7D–E).

Pleon with 5 pleopods composed of basis (sympod), exopod, and endopod (Fig. 6F). Sympods with 1 or 2 medially directed spines, endopods with plumose setae (5 setae on pleopod 1), exopods with plumose setae (4 setae on pleopod 1) and one laterally directed seta (short on pleopod 1, longer on pleopods 2–5); setae on endopods and exopods reduced in number on pleopod 5. Pleotelson quadrangular, endopods approximately twice as long as exopods, basis with 1 or 2 posterior setae, endopods and exopods with terminal setae (Fig. 5A–B).

Immature female (Figs. 1, 8). Maximal body length 2.36 mm (from pereonal lobe 2 to pereon-



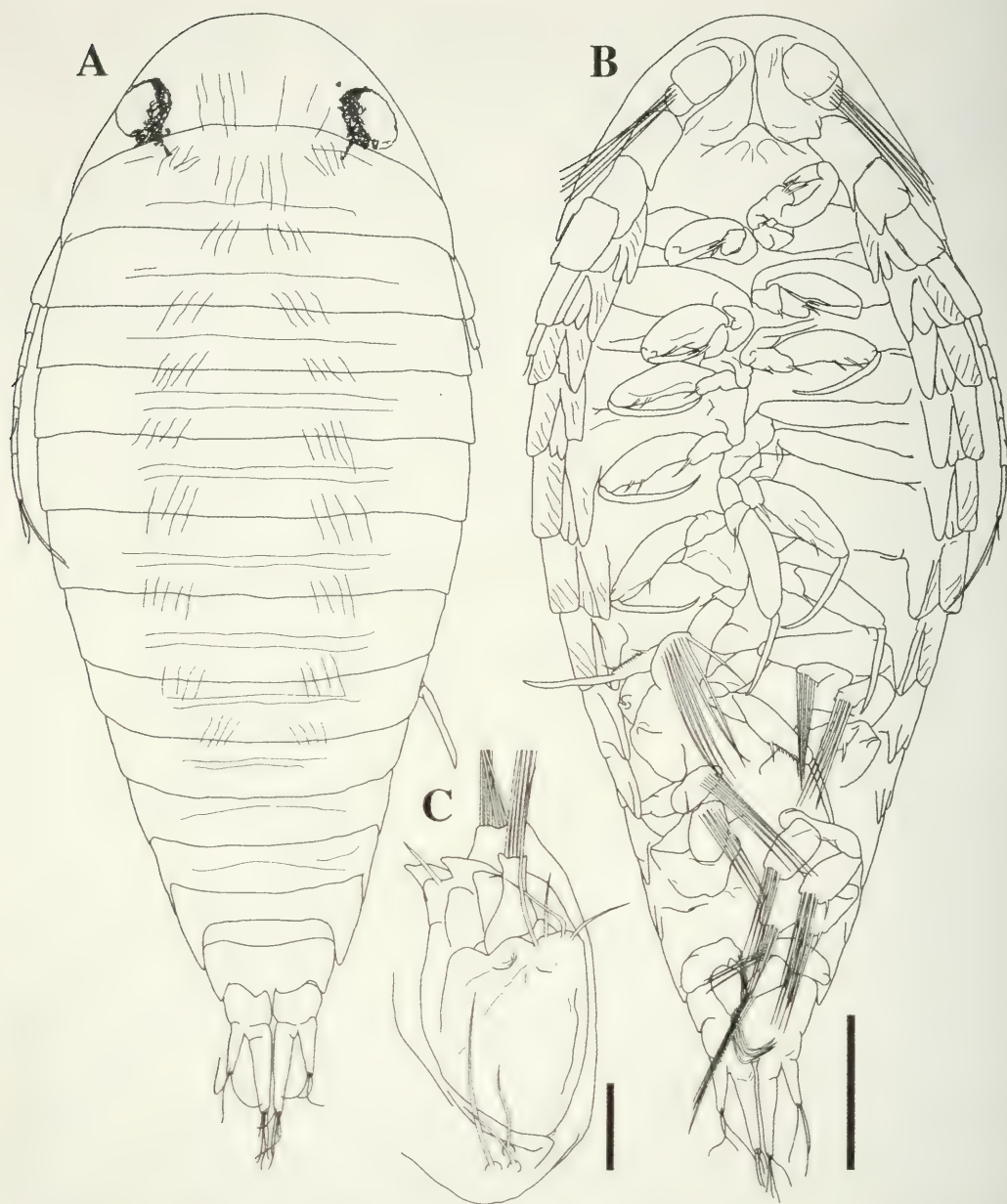


FIGURE 5. *Cabirops bombyliophila* sp. nov., male, 0.91 mm. CASIZ 170231, holotype. A, dorsal view; B, ventral view; C, first antenna, ventral view (terminal setae only partially drawn). Scale = 150  $\mu$ m (A, B), 25  $\mu$ m (C).

al lobe 7), maximal width 1.81 mm, pleon length 0.73 mm. In lateral aspect, body highly curved ventrally, forming U-shape with head region and pleon apposed (Fig. 8). Slight light-brown pigmentation on rostrum (Fig. 8B). Pereon with 7 pereonal lobes, lobes 4–6 largest, on right side all lobes rounded (Fig. 8A), on left side lobes 1–3 rounded and lobes 4–6 with semi-circular depressions (Fig. 8B). Faint indication of segmentation on ventral side of pereon, no appendages. Pleon

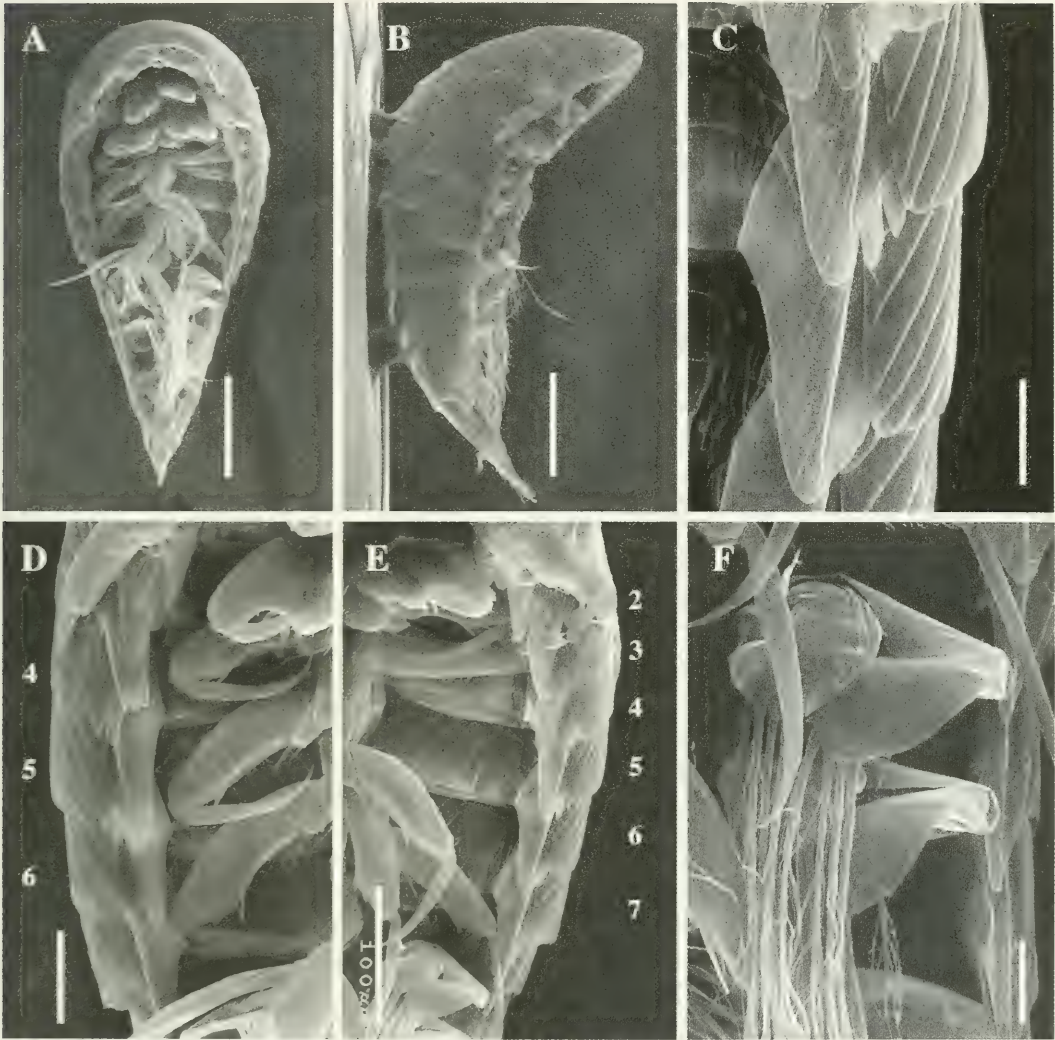


FIGURE 6. *Cabirops bombyliophila* sp. nov., male, 0.91 mm, CASIZ 170231, holotype. A, ventral view; B, lateral view; C, ventral view of segments 5 and 6 showing dentition, left side; D, ventrolateral view of segments 4-6, right side; E, ventrolateral view of segments 2-7, left side; F, left pleopods 1 and 2. Scale = 200  $\mu$ m (A, B), 25  $\mu$ m (C, F), 50  $\mu$ m (D), 100  $\mu$ m (E).

conical in shape, with faint indication of segmentation. Pleon with 4 semi-circular depressions on right side in a trapezoidal configuration (Fig. 8A).

**DISTRIBUTION.**— Found in marsupium of female *Schizobopyrina bombyliaster* sp. nov. ex *Gnathophyllum americanum* from Tonga; 0.6-2.7 m depth.

**ETYMOLOGY.**— The specific name refers to the finding of this hyperparasite in association with the parasite of a bumblebee shrimp of the genus *Gnathophyllum*.

**REMARKS.**— The genus *Cabirops* now contains 17 species (six of these remain unnamed) and this likely represents only a fraction of the species that await description (Sassaman 1985; Boyko and Williams 2004). Sassaman (1985) reviewed the genus and indicated that it could be divided into two groups based on coxal plate dentition. Group one contains species with 2 or 3 denticles on



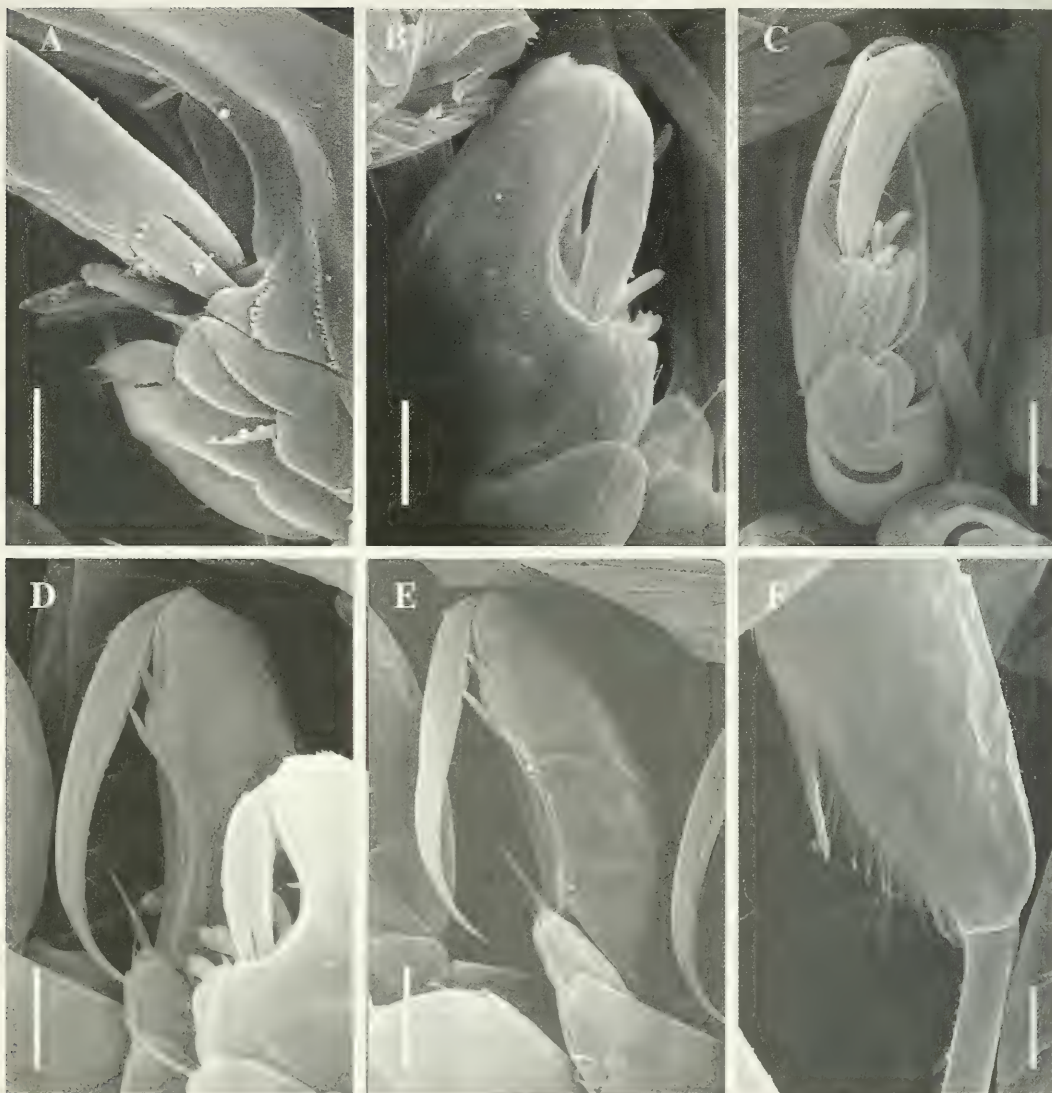


FIGURE 7. *Cabirops bombyliophila* sp. nov., male, 0.91 mm, CASIZ 170231, holotype. A, right pereopod 1; B, left pereopod 2; C, left pereopod 2; D, left pereopod 3; E, left pereopod 4; F, left pereopod 6. Scale = 10 µm (A, F), 20 µm (B, D), 25 µm (C, E).

coxal plates 1–5 and 1 denticle on coxal plates 6 and 7, group two contains species with 2 or 3 denticles on all coxal plates. Members of group one parasitize hosts of the subfamilies Pseudioninae or Orbioninae while members of group two are found on hosts of the subfamilies Ioninae and Bopyrinae. While the morphology of *Cabirops bombyliophila* sp. nov. places it in group one (exhibiting only one denticle on plates 6 and 7), the species is a parasite of a bopyrine host. Such discrepancy is not surprising considering recent studies on *Cabirops* species from the Bahamas have indicated two species with dentition patterns unlike those in either group (Boyko and Williams 2004). In addition, other characters such as the dactyli of pereopods 1 and 2 (bifid vs. simple) and internal apophysis on article 2 of antennae 2 (strong vs. weak) differ between groups.



*Cabirops bombyliophila* sp. nov. most closely resembles *C. codreanui* Bourdon, 1966, *C. montereyensis* Sassaman, 1985, and *C. orbionei* Bourdon, 1972 but can be distinguished from these species based on the dentition pattern (3 denticles on coxal plate 1 in *C. bombyliophila* sp. nov. vs. two denticles on coxal plate 1 in *C. codreanui*, *C. montereyensis*, and *C. orbionei*). In addition, *C. codreanui* and *C. montereyensis* are parasites of pseudionines while *C. orbionei* is found on orbionines; however, due to the potentially large number of undescribed *Cabirops* species, conclusions on the degree of host specificity are probably premature. *Cabirops bombyliophila* sp. nov. is further distinguished from *C. montereyensis* by exhibiting a blunt tip on the dactyli of pereopods 6 and 7 (bifid dactyli are present in *C. montereyensis*). Finally, the apophysis on article 2 of antennae 2 is strong in *C. bombyliophila* sp. nov. but weak in *C. orbionei*. *Cabirops bombyliophila* sp. nov., *C. montereyensis*, and *C. orbionei* are apparently the only species in the genus to exhibit a setal comb on the dactyl of pereopod 3; however, as indicated by Sassaman (1985), this feature may have been overlooked in earlier descriptions.

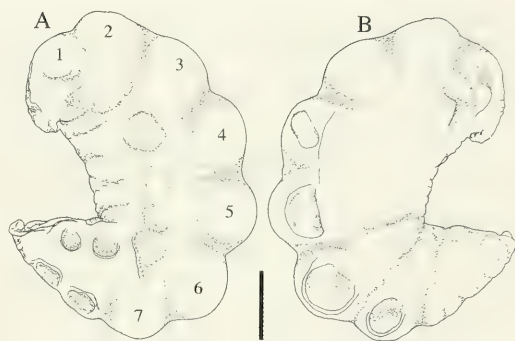


FIGURE 8. *Cabirops bombyliophila* sp. nov., female, 2.36 mm, CASIZ 170232, allotype. A, view of right side, numbers indicate dorsal pereopodal lobes; B, view of left side. Scale = 500  $\mu$ m.

#### ACKNOWLEDGMENTS

Dr. Bob Van Syoc (CASIZ) provided loan of specimens and kindly hosted a brief visit by CBB to CASIZ. Dr. Alain Crosnier (MNHN) is thanked for inviting CBB to examine material in the MNHN collections. We thank Ms. Lauren M. Schuerlein (Hofstra University) for her work on the final plates. Financial support from Hofstra University to JDW is greatly appreciated.

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## Taxonomic Status of *Rhacophorus taronensis* Smith, 1940

Jeffery A. Wilkinson<sup>1,3</sup> and Dingqi Rao<sup>2</sup>

<sup>1</sup>Department of Herpetology, California Academy of Sciences, 875 Howard Street, San Francisco, California 94103; <sup>2</sup>Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, Yunnan, China 650223; <sup>3</sup>H.T. Harvey & Associates, 3150 Almaden Expressway, Suite 215, San Jose, CA 95118

*Polypedates gongshanensis* (Yang and Su, 1984), described as endemic to the Gaoligong Mountains of western Yunnan Province, China, is demonstrated to be a junior synonym of *Rhacophorus taronensis* Smith, 1940, the latter known only from the type specimen collected in northern Myanmar. This poorly known species is revisited, and new data derived from comparisons of the original descriptions, examinations of the type specimens of *R. taronensis* and *P. gongshanensis*, and newly acquired specimens from Myanmar and China are presented.

Smith (1940)<sup>1</sup> described a new species of *Rhacophorus* based on a single specimen (BMNH 1947.2.8.17) collected by R. Kaulback in the north of Myanmar (Patsarlamdam, Taron Valley; N 27°43', E 98°10') on 01 June 1939. He states that this new species (*R. taronensis*) is related to *R. bimaculatus* but differs by having less extensive webbing of the fingers, the absence of a dermal projection on the heel, and different coloration. He gives a snout-vent length of 78 mm and also presents a drawing of the right hand (Smith 1940, fig. 3). Since then, no new specimens of *R. taronensis* have been reported.

Yang and Su (1984)<sup>2</sup> described a new species of *Rhacophorus* from the southern Gaoligong Mountains of western Yunnan Province, China. They compared their specimens only to *Rhacophorus feae* (now *Polypedates feae* fide Frost 2002), probably due to the similar brown line extending from the tip of the snout to behind the tympanum that is present in both their specimens and *R. feae*. Their specimens differed from *R. feae* by the webbing of the first and second fingers being restricted to the base and only one-third webbing between the remaining fingers; the heels overlapping when the legs are at right angles to the body; and by the presence of creamy-colored spots on the flank and inner and outer sides of the thigh. Based on these differences, they concluded that these specimens represented a new species, *R. gongshanensis*, believed to be restricted to the

<sup>1</sup> Original description (Smith 1940): "Vomerine teeth in strong, almost transverse, groups, commencing at the inner margin of the choanae. Head broader than long, much depressed; snout rounded, scarcely projecting beyond the mouth, shorter than the eye; canthus rostralis distinct; loreal region oblique, feebly concave; nostril a little nearer the tip of the snout than the eye, nearly as broad as the interorbital space, broader than the upper eyelid; tympanum very distinct, 4/5 the diameter of the eye, close to it. Outer three fingers with very large discs, which are as broad as long and as large as the tympanum; more than half webbed, the membrane reaching the disc of the 4th finger and that of the 2nd on the outer side; toes fully webbed, their discs smaller than those of the fingers; the tibio-tarsal articulation reaches to between the eye and the tip of the snout; subarticular tubercles of both fingers and toes strongly developed; a short oval inner metatarsal tubercle; no outer. Skin smooth above, that of the belly and hinder part of the thighs coarsely granulate. A dermal fringe, feebly distinct, on the outer side of the fore-arm, tarsus and foot. Bluish above, green in life, with small black spots; lower parts whitish, thickly speckled with dark grey; hinder part of thighs black with white spots. From snout to vent 78 mm."



Gaoligong Mountains. Subsequently, Fei, Ye, and Huang (1990) placed *R. gongshanensis* in the genus *Polypedates* without explanation.

In the process of identifying specimens of *Rhacophorus* collected in northern Myanmar in 2002 by the Myanmar Herpetological Survey Project (a collaborative project of the California Academy of Sciences, Smithsonian Institution, and the Nature and Wildlife Conservation Division, Forest Department, Myanmar), the holotype of *R. taronensis* (BMNH 1947.2.8.17, re-catalogued from BM 1940.6.1.39; Figs. 1A, C, E) was examined. It was immediately evident that the holotype was similar in appearance to specimens of *P. gongshanensis* from Baoshan Prefecture, Yunnan Province, China, collected by a California Academy of Sciences (CAS) and Kunming Institute of Zoology (KIZ) field expedition in 2003.

## METHODS AND MATERIALS

In order to determine whether *R. taronensis* and *P. gongshanensis* are conspecific, the holotypes of *R. taronensis* and *P. gongshanensis* (KIZ 810485; Figs. 1B, D, F) were examined and compared to each other and to the original descriptions. In addition, they were compared with a paratype of *P. gongshanensis* (KIZ 810555) and newly collected specimens from Myanmar.

Specimens recently collected in Myanmar are housed in the collections of the Department of Herpetology, CAS and the Myanmar Biodiversity Museum (MBM), Hlawga, Myanmar. Newly collected specimens from Baoshan Prefecture, China (GLGS field numbers in materials examined section below), are as yet not available for measurements, but eventually they will be housed in the

<sup>2</sup> Literal translation of original description in Chinese (Yang and Su 1984) — “The body is medium in size, the largest among the 6 male specimens is only 72.2 mm long, the only female specimen is 81.5 mm long. The head is slightly longer than wide in males, but wider than long in the female; the rostrum sharply angles downward from the nostril forward, the canthus rostralis is obvious, the loreal region slants slightly outward, the surface of the loreal region is concave; the nostrils are located midway between the tip of the snout and eyes; the internarial distance is shorter than the interorbital distance; the top of head is flat; the tympanum is elliptical and close to the eye, with a vertical diameter  $\frac{1}{2}$  of the diameter of the eye, and close in size to the disc of the third finger; the back of the tongue has a deep notch; vomerine teeth are not curved into an arch, the lateral end is slightly beyond the anterior angle of the internal nares, slightly inclined caudally but does not pass the posterior edge of the internal nares.

“The forearm of the male frog is strong, that of the female is slightly weaker, the length of the forearm and hand is slightly beyond half of the body. Fingers are flattened, and rank according to size from big to small, as 3, 4, 2, 1. The disc is wide and straight at terminal end, with a transverse groove at the tip. The disc of the first finger is small; the second, third and fourth fingers are approximately 1:1 webbed, the second finger is webbed to the subarticular tubercle, the third and fourth fingers are webbed to the distal end of the subarticular tubercle, the first and second fingers are only webbed at the base; the inner edge of the first finger and outer edges of the second and third fingers with obvious marginal webbing; the tubercles at the distal end of the third and fourth fingers are bigger than those at the proximal end; the inner edge of the first finger is enlarged at the base in a transverse direction. The hind limbs are 1.5 times that of the body size, the specimen KIZ 810485 is 1.7 times, tibiotarsal articulation reaches to the middle or anterior edge of eyes, the left and right heels overlap; feet are shorter than the tibia (6 males), but reverse for the female; webbing on the toes are relatively well developed to the base of the disc, only the fourth toe webbed to the distal subarticular tubercle; the subarticular tubercles are small and round, inner metatarsal tubercle is small, flat and elliptical, no outer metatarsal tubercle.

“The male frog is dotted with white asperities on the dorsal aspect of the body and hind limbs, but the female frog with fewer asperities than the male; dense flat areolation on the ventral surface, the areolation on the lower jaw, throat, and pectoral region is smaller than other areas, the front of the lower jaw of the female frog is smooth without tubercles, the supratympanic fold is linear but slopes slightly backward.

“In life, the pupil is a horizontal ellipse, blue-black, iris is greenish yellow. Upper surface of head, body, and the four limbs is grass-green, with sparsely scattered small brown spots. The flank and inner and outer side of thigh with many creamy yellow spots, big or small, with dark reddish brown to purple edges. The canthus rostralis, lateral edge of eyelid, and supratympanic fold are light brown. The anterior half of the fingers and toes are violet on dorsum, the posterior half remains grass-green. The supracloacal region, from the tibiotarsal articulation to the base of the fifth toe, and outer side of forearm to the base of fourth finger with a yellowish fine linear dermal ridge. Ventral surface light brown to purple, with scattered deep dark spots.”

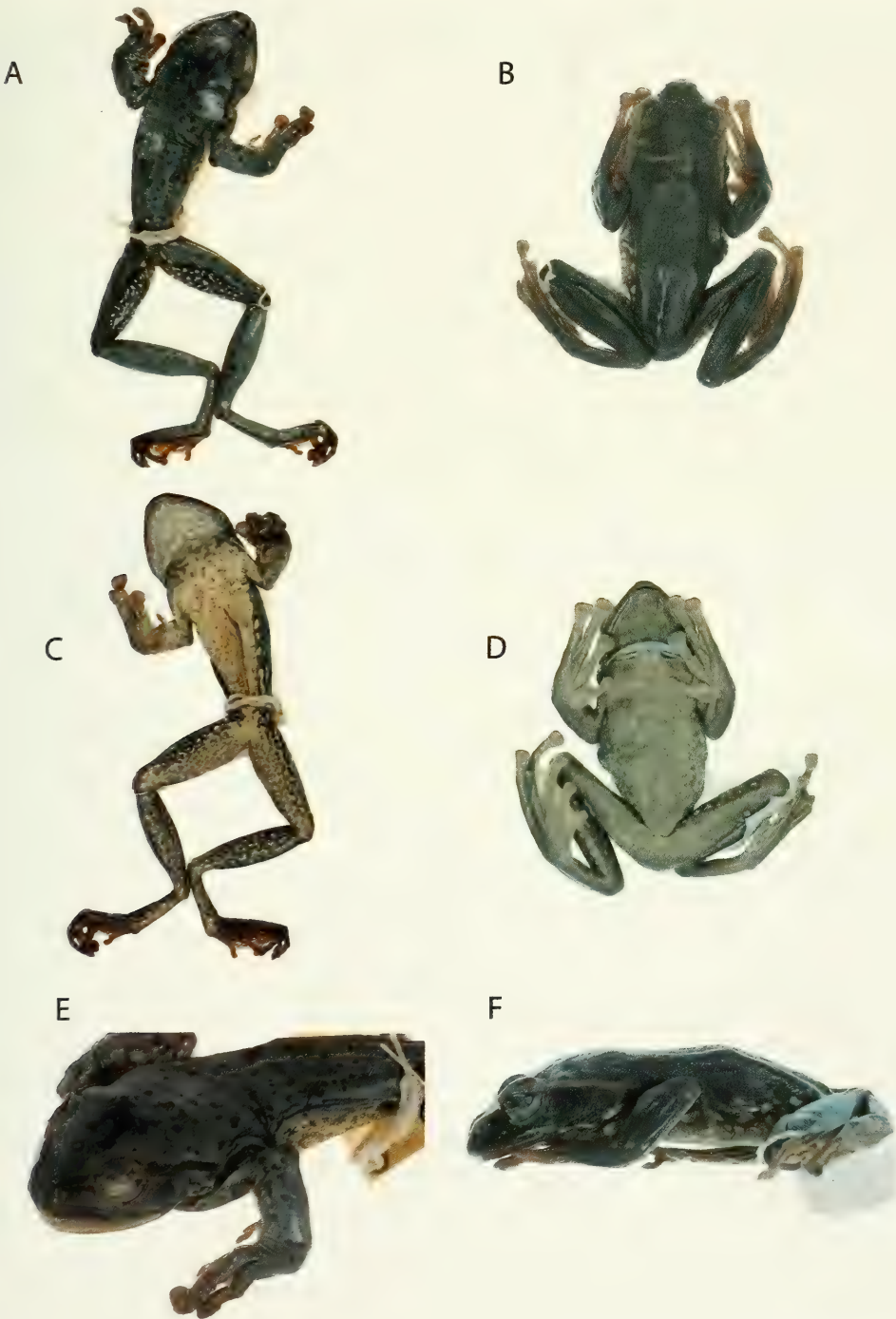


FIGURE 1. Dorsal, ventral, and lateral views respectively of the holotype (BMNH 1947.2.8.17) of *Rhacophorus taronensis* (A, C, E) and the holotype (KIZ 810485) of *Polypedates gongshanensis* (B, D, F).

collection of the Department of Herpetology, CAS and the Department of Herpetology, KIZ. They have been included to report locality data. After tissues were removed from the recently collected specimens (Myanmar and China), the specimens were fixed in 10% buffered formalin before being transferred to 70% ethanol. Latitude and longitude were recorded with a Garmin 12 GPS (WGS84).

Sex was determined by the presence or absence of vocal apertures, or the presence or absence of eggs within the abdominal cavity. Measurements were taken using dial calipers to the nearest 0.1 mm as follows: snout-vent length (SVL, from tip of snout to vent); head length (HL, from tip of snout to hind border of angle of jaw); head width (HW, width of head at its widest point); internarial distance (IND, distance between nares); interorbital distance (IOD, minimum distance between upper eyelids); upper eyelid width (UEW, maximum upper eyelid width); snout length (SL, from anterior border of eye to tip of snout); eye diameter (ED, horizontal length between orbital borders of eyes); distance from nostril to eye (DNE, from nostril to anterior border of eye); tympanum diameter (TD, greatest diameter); forelimb length (FLL, from elbow to tip of third finger); first finger length (FFL, from palmer end of inner metacarpal tubercle to tip of finger); third finger length (TFL, from base point between third and fourth fingers to tip of finger); hand length (HAL, from base of outer palmer tubercle to tip of third finger); thigh length (THL, from vent to knee); tibia length (TIL, from knee to foot); foot length (FL, from proximal end of metatarsal tubercle to tip of fourth toe); fourth toe length (FTL, from distal end of third subarticular tubercle to tip of toe); inner metatarsal length (IML, at point of greatest length); width of disk of third finger (3FDW, greatest horizontal width); and width of disk of fourth toe (4TDW, greatest horizontal width).

## RESULTS

**COMPARISON OF TYPES.**— The holotype of *R. taronensis* (female) is similar to the holotype of *P. gongshanensis* (male) in shape, color, and pattern. However, the holotype of *R. taronensis* is longer (SVL 76.6) than the holotype of *P. gongshanensis* (SVL 70.5), the head is wider than long (versus longer than wide in holotype of *P. gongshanensis*), the nostrils are nearer to the tip of the snout than the eyes (versus midway between eye and tip of snout in holotype of *P. gongshanensis*), and the third finger is longer with a wider disc (versus shorter with a narrower disc in holotype of *P. gongshanensis*). The SVL is also longer and the head wider than long for the female paratype of *P. gongshanensis* (CIB 810723; referred to as the allotype in Yang and Su) and a female specimen (CAS 224382) in this study, indicating that these are sexually dimorphic characters. The length of the third finger and width of the disc of third finger are not mentioned for the female paratype of *P. gongshanensis* in Yang and Su (1984) but in the aforementioned female specimen in this study are similar to the holotype for *R. taronensis* and different from the male specimens (Table 1), indicating that these may also be sexually dimorphic characters. The relative location of the nostrils was also nearer to the tip of the snout in the aforementioned female specimen and most of the male specimens, but closer to the eyes in two male specimens (KIZ 810555, CAS 224371) suggesting that this character is not sexually dimorphic.

To detect whether other species of *Rhacophorus* also possess the aforementioned apparent sexually dimorphic characters, specimens of *R. owstoni* were measured for SVL, HL, HW, TFL, and 3FDW. All female specimens ( $N = 14$ ) were larger ( $SVL \times = 58.93$ ,  $\sigma = 4.13$ ) than the male specimens ( $N = 12$ ;  $SVL \times = 46.86$ ,  $\sigma = 2.21$ ). Also, several but not all female specimens possessed a head slightly wider ( $HW \times = 22.46$ ,  $\sigma = 1.56$ ) than long ( $HL \times = 22.28$ ,  $\sigma = 1.13$ ), whereas, all male specimens possessed a head slightly longer ( $HL \times = 17.92$ ,  $\sigma = 0.80$ ) than wide ( $HW \times = 17.47$ ,  $\sigma = 0.76$ ). Also, the length of the third finger and the width of the disc of the third finger were on average respectively longer and wider in the female specimens ( $TFL \times = 9.45$ ,  $\sigma = 0.73$ ,



TABLE 1. Measurements of the holotype and newly collected specimens of *Rhacophorus taronensis* and the holotype and a paratype of *Polypedates gongshanensis*. Top values for holotypes are original measurements in Smith (1940) and Yang and Su (1984).

	sex	SVL	HL	HW	IND	IOD	UEW	SL	ED	DNE	TD	FLL	FFL	TFL	HAL	THL	TIL	FL	FTL	IML	3FDW	4TDW
BMNH 1947.2.8.17		78																				
(holotype)	F	76.6	24.4	26.8	6.4	7.1	5.6	10.7	9.6	6.2	5.6	42.6	13.7	19.6	26.3	34.9	39.7	35.2	17.2	4.2	5.6	3.6
CAS 224382	F	73.1	24.5	25.3	5.9	8.4	7.2	11	8.3	6.4	5	40.9	12.9	17.1	25.7	39.9	36.4	33.5	17.2	3.3	5.9	4
Average		74.9	24.5	26.1	6.1	7.7	6.4	10.9	8.9	6.3	5.3	41.7	13.3	18.3	26	37.4	38.1	34.4	17.2	3.8	5.8	3.8
Ratio of SVL			32.7	34.8	8.1	10.3	8.5	14.6	11.9	8.4	7.1	55.7	17.8	24.4	34.7	49.9	50.9	45.9	23	5.1	7.7	5.1
KIZ 810485		69	25	24.5	7.8	8.5	6.8	12	9.5		4.9	40			27	35.2		34			5	
(holotype)	M	70.5	23.5	23.1	6.4	7.6	6.4	11.2	8.6	5.5	5.5	40.4	12.2	16.8	25.3	35.1	34.6	33.9	17.3	3	5	3.8
CAS 224371	M	67.7	24.2	22.8	6.5	6.8	4.7	11.8	7.9	5.7	5.1	35.7	10.3	14.2	20.6	32.6	29.5	27.1	13.3	3.3	4.3	3.7
CAS 224377	M	62.4	22.1	20.7	5.3	6.3	5.8	10.5	7.6	5.9	4.5	34.2	9.8	13.5	20.7	31.6	29.6	27.6	13.7	2.6	3.7	2.7
KIZ 810555																						
(paratype)	M	61.9	21.6	21.3	6.5	6.9	5.1	10	7.3	5.1	5.2	35.2	10.7	15.3	21.8	32.9	31.1	29.7	13.9	3.2	4.5	3.3
CAS 224379	M	60.5	21.3	19.8	5.5	7.5	5.3	9.9	8	5.9	4.7	34.1	9.9	13.4	22.1	32.8	30.7	28.2	14	1.9	4.2	3.1
MBM-JBS 11793																						
M	60.5	20	19.4	4.5	6.5	4.9	9.4	6.8	5.5	4.6	31.5	9.5	12.7	19.3	30.5	28.1	26.1	13.1	2.8	3.6	2.4	
CAS 224373	M	59.7	20.9	20.3	5.2	5.8	5	9.9	7.6	5.5	4	33.7	9.9	13.5	20.4	30.3	29.8	26.4	14.1	2.5	3.7	3
CAS 224372	M	59.2	20.3	19.3	4.8	6.4	4.6	9.6	6.9	5.4	4.5	30.7	9.9	12.2	18.8	29.9	27.6	25.8	13	1.9	3.4	2.9
CAS 224370	M	57.4	20.1	19.7	5	5.9	4.6	9.4	6.4	5.9	4.7	31.9	9.6	13.1	19.9	29.9	26.8	27.1	13.5	2.4	4.2	3.2
CAS 224369	M	55.7	19.1	18.6	4.7	6.3	4.4	8.8	6.8	4.7	3.9	28.3	8.6	11.8	18.5	28.1	27.7	23.1	11.5	2.4	2.8	1.8
Average		61.5	21.3	20.5	5.4	6.6	5.1	10	7.4	5.5	4.7	33.6	10	13.6	20.7	31.4	29.5	27.5	13.7	2.6	3.9	3
Ratio of SVL			34.6	33.3	8.7	10.7	8.3	16.2	12	8.9	7.6	54.6	16.2	22.1	33.6	51.1	47.9	44.7	22.2	4.2	6.3	4.9

ratio to SVL 0.20; 3FDW  $\times$  = 2.59,  $\sigma$  = 0.32, ratio to SVL 0.06) than male specimens (TFL  $\times$  = 12.70,  $\sigma$  = 1.16, ratio to SVL 0.22; 3FDW  $\times$  = 3.88,  $\sigma$  = 0.47, ratio to SVL 0.07), though these differences were more pronounced in the larger females, indicating that they may merely be ontogenetic.

Most of the characters given in the description by Yang and Su (1984) and Smith (1940) are consistent with both holotypes of *R. taronensis* and *P. gongshanensis*, with the following exceptions: (1) the position of the tibiotarsal articulation and the amount of webbing between the fingers for both the holotypes of *R. taronensis* and *P. gongshanensis* differ from the description by Yang and Su (1984) and more closely resemble the description in Smith (1940) in that the tibiotarsal articulation reaches to between the eye and end of the snout and the fingers are more than 1/2 webbed; (2) the relative size of the tympanum and amount of webbing on the toes in both the holotypes of *P. gongshanensis* and *R. taronensis* differ from the description by Smith (1940) and more closely resemble the description in Yang and Su (1984) in that the tympanum is only slightly over half the diameter of the eye (Table 1) instead of 4/5<sup>th</sup>, and the toes are not fully webbed but reach only to the distal subarticular tubercle on the fourth toe; and (3) the holotype of *R. taronensis* is smaller than the reported size of the female paratype of *P. gongshanensis* by 3.5 mm (from Smith, 1940) or 4.9 mm (measurements taken in this study).

Measurements of all specimens examined are given in Table 1. These measurements differ slightly from those given in Yang and Su (1984) for the holotype of *P. gongshanensis* (greatest dif-

ference being 1.7 mm for hand length), and given in Smith (1940) for the holotype of *R. taronensis* (a smaller snout-vent length in this study). Measurements of the holotype of *R. taronensis* and the holotype and a paratype of *P. gongshanensis* are generally smaller than those reported in Yang and Su (1984) and Smith (1940). This may be due to shrinkage of the type specimens between measurements or different standards used in measuring. The nine specimens newly collected from Myanmar are on average smaller than those collected by Yang and Su (1984). However, the ratios of average measurements of each structure to average snout-vent length for the males are similar between the Yang and Su (1984) study and this study.

**VARIATION.**— Further observations were made on specimens newly collected from Myanmar. On several specimens (CAS 224370–224371, 224382, 224397, MBM-JBS 11793; Joseph B. Slowinski field number to be deposited in the MBM) the spotting on the flanks is white, more reticulate, and continues onto the ventral surface (Fig. 2). The brown spotting on the back may be very extensive (CAS 224371, 224377, MBM-JBS 11793) (Fig. 2) or absent (CAS 224369–224370, 224379).



FIGURE 2. From a color transparency of *Rhacophorus taronensis* (MBM-JBS 11793).

The discs on the fingers of the females are relatively larger than those of males but the snout lengths are relatively shorter. The rostrum of some specimens (CAS 224371–224372, 224377) is spatulate in form, from the nostril to the tip of the snout. All specimens have two strong brown dorsolateral lines that bifurcate at the tip of the snout and continue along the canthus rostralis, lateral edge of eyelid, supratympanic fold, and terminating behind the insertion of the forelimb (Fig. 2).

The preceding data demonstrate that the two types are the same species. Variation between the types and the other specimens in this study can be attributed to sexual dimorphism and normal ranges of differences within a species. *Polypedates gongshanensis* is, thus, a subjective junior synonym of *R. taronensis*.

**DISTRIBUTION.**— Based on records for the type specimens and recent collections in both China and Myanmar, at present, *R. taronensis* occurs only in the mountainous regions of the northern portion of Kachin State, Myanmar and to the south in Baoshan Prefecture, Yunnan Province, China (Fig. 3). Fei (1999) gives a distribution for *P. gongshanensis* extending from Baoshan Prefecture north along the Chinese side of the China-Myanmar border into Gongshan County, Nujiang Prefecture, indicating that this species occurs throughout the border regions of China and Myanmar. However, this distribution has not been confirmed by voucher specimens or recent surveys in these areas.

**MATERIAL EXAMINED.**— BMNH 1947.2.8.17, holotype of *R. taronensis*, Myanmar, Patsarlamdam, Taron Valley; 27°43'N, 98°10'E; CAS 224369–224372, MBM-JBS 11793, Myanmar, Kachin State, Putao District, Nagmung Township, Hkakabo Razi National Park, Nga War Village, 27°49'44.1"N, 97°45'59.3"E; CAS 224377, 224379, 224382, Myanmar, Kachin State, Putao District Nagmung Township, Hkakabo Razi National Park, Nga War Village, 27°49'04.1"N, 97°46'41.3"E; KIZ 810485, holotype of *Polypedates gongshanensis*, and 810555, paratype, China,



Yunnan Province, Baoshan Prefecture, Pumanshao; Gaoligongshan (GLGS) field numbers to be deposited in the CAS and KIZ, GLGS 1038–1039, 1047, 1049–1050, 1059–1063, 1065–1068, 1070–1079, China, Yunnan Province, Baoshan Prefecture, Tengchong County, Xiao Di Fang Village, 24°52'12.2"N, 98°45'13.4"E; *Rhacophorus owstoni*, CAS 211426–211447, 211449–211452, Japan, Okinawa Prefecture, Ryukyu Islands, Iriomote Island.

### ACKNOWLEDGMENTS

We thank U Shwe Kyaw, Director General, Forest Department, Ministry of Forestry, and U Khin Maung Zaw, Director, Nature and Wildlife Conservation Division, Forest Department, Ministry of Forestry, for their continued support of the Myanmar Herpetological Survey Project. We thank Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein, and Hla Tun of the Myanmar Herpetological Survey Field Team for their efforts in collecting, and personnel of the Baoshan Nature Reserve for their help during the joint 2003 CAS/KIZ expedition. We also thank the British Museum for loaning and Edwin N. Arnold for hand carrying the type specimen. Fieldwork was supported by a National Science Foundation Grant (DEB-9971861) to Joseph B. Slowinski and George R. Zug, a National Science Foundation Grant (DEB-0103795) to Joseph B. Slowinski and Peter W. Fritsch, and a National Geographic Society Grant (7340-02) to Peter W. Fritsch. Dong Lin assisted in creating Figure 1, Hla Tun provided Figure 2, and Michelle S. Koo provided Figure 3. Lihua Zhou provided the translation of the Chinese text. Jens V. Vindum, Guinevere O.U. Wogan, and George R. Zug critically read and provided valuable comments on the manuscript.

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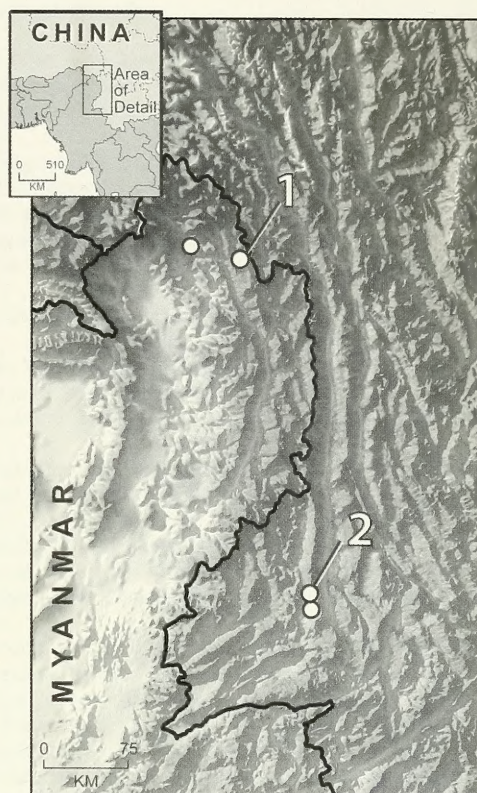


FIGURE 3. Map of known localities of *Rhacophorus taronensis* based on specimens used in this study. The type localities for *R. taronensis* and *P. gongshanensis* are indicated by the numbers 1 and 2 respectively.





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